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# PRESENT KNOWLEDGE OF RICE GENETICS AND CYTOGENETICS

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## FOREWORD

With this bulletin, The International Rice Research Institute is initiating a new series of technical publications designed to disseminate scientific information accumulated by its staff members and visiting scientists. This series will constitute rather complete reviews or research projects that are too complex to be published in the usual scientific journals that serve as outlets for shorter research papers. It is hoped that these bulletins, together with the series of Institute-sponsored international symposia on rice and the international bibliography of rice research, will contribute toward a better understanding of the rice plant.

In this bulletin, Dr. Te-Tzu Chang summarizes the latest information on rice genetics, cytogenetics, and allied fields. Attention is given to the application of basic findings in genetics and cytogenetics to varietal improvement.

This review fills a long-felt need to bring together in one medium the voluminous, multi-language literature on these important subjects. Its organized presentation of outstanding findings will assist students in rice breeding, genetics, and cytogenetics to appreciate the orderly development of understanding toward our present knowledge of these subjects. Its broad coverage also will serve the needs of rice agronomists, physiologists, pathologists, entomologists, and other interested workers.

The Institute expects that this bulletin, along with other monitoring services channelled through the International Rice Commission Newsletter, will help further establish uniformity in the genetic nomenclature of rice.

Robert F. Chandler, Jr.
Director
The International Rice Research Institute

Los Baños, The Philippines
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# PRESENT KNOWLEDGE OF RICE GENETICS AND CYTOGENETICS[1]

The purpose of this review is to summarize our understanding of the genetical and cytogenetical aspects of the cultivated rices and their related species. As in any branch of knowledge, there is some disagreement among rice workers on various points concerning the taxonomy, genetics and cytogenetics of rice. Divergent views on controversial issues are presented with emphasis on the more widely accepted current hypotheses.

## Species of Oryza and Species Relationships

### Species

The classification and nomenclature of species in the genus Oryza is an unsettled issue. The genus includes approximately 20 valid species, the exact number depending upon the particular scheme of classification and nomenclature one follows. The commonly accepted taxa, their chromosome numbers and their distribution are given in Table 1.

Table 1. Chromosome Number and Distribution of Oryza Species

| Species or Form | Chromosome No. (2n) | Distribution |
|---|---|---|
| O. alta Swallen | 48 | Central and South America |
| O. angustifolia C. E. Hubbard | - | Africa |
| O. australiensis Domin | 24 | Australia |
| O. brachyantha A. Chev. et Roehr. | 24 | West and Central Africa |
| O. breviligulata A. Chev. et Roehr. | 24 | West Africa |
| O. coarctata Roxb. | 48 | Burma, India and Pakistan |
| O. eichingeri A. Peter | 24, 48 | Ceylon and East Africa |
| O. glaberrima Steud. | 24 | West Africa |
| O. grandiglumis (Doell) Prod. | 48 | South America |
| O. granulata Nees et Arn. ex Hook f. | 24 | South and Southeast Asia |
| O. latifolia Desv. | 48 | Central and South America |
| O. longiglumis Jansen | 48 | New Guinea |
| O. malampuzhaensis Krish. et Chand. | 48 | India |

[1]The survey of literature pertaining to this review was concluded in May 1964.

Table 1. (cont'd.)

| Species or Form | Chromosome No. (2n) | Distribution |
|---|---|---|
| O. meyeriana (Zoll et Mor. ex Steud.) Baill. | 24 | Southeast Asia |
| O. minuta J. S. Presl ex C. B. Presl | 48 | Southeast Asia |
| O. officinalis Wall. ex Watt | 24 | South and Southeast Asia |
| O. perennis Moench subsp. balunga[1] | 24 | South and Southeast Asia |
| O. perennis Moench subsp. barthii[1] | 24 | Africa |
| O. perennis Moench subsp. cubensis[1] | 24 | South America and West Indies |
| O. perrieri A. Camus | 24 | Malagasay |
| O. punctata Kotschy ex Steud. | 24, 48 | Africa |
| O. ridleyi Hook f. | 48 | Southeast Asia |
| O. sativa L. | 24 | Asia, Africa, Australia, Europe, the Americas |
| O. sativa L. v. fatua Prain[2] or O. sativa L. f. spontanea Roschev.[2] | 24 | Asia, Australia, South America, Malagasay |
| O. schlechteri Pilger | - | New Guinea |
| O. stapfii Roschev. | 24 | West Africa |
| O. tisseranti A. Chev. | 24 | Central Africa |

[1]Temporary designations.

[2]Name of uncertain application.

Roschevicz (1931)[3] recognized 19 species of Oryza. Roschevicz's classification scheme was later modified and improved by Chevalier (1932)[3] and Chatterjee (1948). Chevalier listed 22 species and Chatterjee recognized 23 species. Recently, Tateoka (1962a, 1963) presented a revised classification scheme and recognized 22 species. Sampath (1962) also proposed 22 species of Oryza on the basis of morphological and cytogenetical differences. A list of Oryza species recognized by the above workers and their synonyms under the four classification schemes are given in Appendix A.

[3]English translation of these papers are now available at the IRRI Library.

At a Symposium on Rice Genetics and Cytogenetics held at The International Rice Research Institute in 1963, a committee on taxonomy recommended that 19 distinct and valid species be recognized. They are O. alta, O. angustifolia, O. australiensis, O. brachyantha, O. breviligulata, O. coarctata, O. eichingeri, O. glaberrima, O. latifolia, O. longiglumis, O. meyeriana, O. minuta, O. officinalis, O. perrieri, O. punctata, O. ridleyi, O. sativa, O. schlechteri and O. tisseranti. The committee also suggested further study to determine the validity and relationships of O. stapfii, O. granulata, O. grandiglumis, O. malampuzhaensis, and O. ubanghensis to other established species. The same was suggested for the relationships between the taxa commonly designated as O. sativa f. spontanea (or var. fatua) and the Asian, American and African forms of O. perennis. O. subulata was recognized as Rynchoryza subulata (Nees) Baill. The discussion held during the Symposium also revealed the need to incorporate information from the cytogenetical studies of various species and their hybrids, biochemical studies, and biostatistical investigations, to assist in the systematic treatment of Oryza species.

Of the above species, O. sativa L. (common rice) and O. glaberrima Steud. (African rice) are the only two cultivated species. O. sativa is the only species found both in temperate and tropical regions; all others are tropical species. O. sativa is generally considered an annual although it may grow longer than one year under favorable conditions. The following species are reported to be annuals: O. angustifolia, O. brachyantha, O. breviligulata, O. glaberrima, O. perrieri, O. stapfii, and O. tisseranti. The other species are perennials.

## Species Relationships

### Species Groups

Roschevicz (1931) grouped the Oryza species into four sections on the basis of the surface structures of the lemma and palea and the shape of the spikelets. Section Sativa Roschev. included O. australiensis, O. breviligulata, O. glaberrima, O. grandiglumis, O. latifolia, O. longistaminata, O. minuta, O. officinalis, O. punctata, O. sativa, O. schweinfurthiana, and O. stapfii; Section Granulata Roschev. included O. abromeitiana and O. granulata; Section Coarctata Roschev. included O. brachyantha, O. coarctata, O. ridleyi, and O. schlechteri; Section Rynchoryza Roschev. included O. subulata, now reclassified as Rynchoryza subulata (Nees) Baill.

Sampath and Rao (1951) examined the relationships among a number of Oryza species on the basis of morphology, geographical distribution and chromosome number. They suggested that the widely distributed O. perennis was the ancestral form of cultivated species, giving rise to O. sativa in Asia and O. glaberrima in Africa by human selection. They also inferred that O. sativa f. spontanea and O. breviligulata were spontanea types of collateral descent from O. perennis. The species of O. officinalis, O. eichingeri, O. latifolia, O. minuta and O. alta appeared to form another natural group in which polyploidy and geographical distribution had played a role in speciation. O. officinalis was considered the primitive diploid species in this group.

Ghose, Ghatge and Subrahmanyan (1956) divided the genus Oryza into three sections: (1) Section Sativa Ghose included O. sativa, O. glaberrima, O. breviligulata, O. perennis and O. australiensis; (2) Section Officinalis Ghose included O. officinalis, O. minuta, O. eichingeri, O. latifolia and O. alta; and (3) Section Granulata Ghose included O. granulata, O. ridleyi, O. coarctata and O. brachyantha. This grouping was based on comparative morphological and anatomical studies of 12 species and the chromosome pairing and fertility of 12 interspecific hybrids (cf. Ghose et al. 1956).

Portéres (1956) postulated that the tetraploid species of O. latifolia, O. alta, O. minuta and O. punctata were derived from the diploid O. officinalis.

The morphological relationships among 16 Oryza species were studied biometrically by Morishima and Oka (1960), using Sokal's methods of correlation coefficients based on measurements of 42 characters. The results are summarized in Figure 1 which indicates the closeness among species.

According to Morishima and Oka (1960), Roschevicz's section Sativa is divisible into two groups: The first group Sativa includes the species O. sativa, O. breviligulata, O. glaberrima, O. perennis and O. sativa f. spontanea; the second group Officinalis includes O. officinalis, O. minuta, O. alta, O. latifolia, and O. eichingeri. This scheme of division agrees with the previous one suggested by Sampath and Rao (1951) and a recent one postulated by Bouharmont (1962a).

Morishima and Oka's studies further suggested that the group Sativa is divisible into two minor groups or series: The first series includes O. sativa,

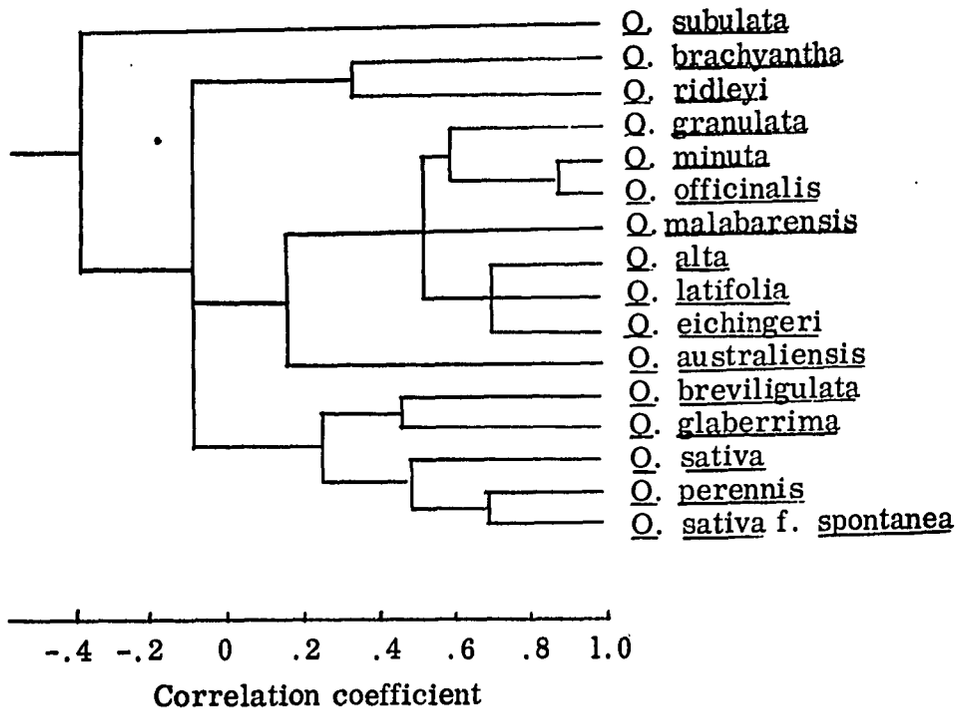


**Figure 1.** Diagram of relationships obtained from correlation matrix II (based on 42 characters).

O. sativa f. spontanea, and O. perennis; the second series contains O. glaberrima and O. breviligulata. Hybrids between these two series were generally highly sterile (Sampath and Rao 1951, Nezu et al. 1960, Yeh and Henderson 1961a, Li, Weng, Chen and Wang 1962, Bouharmont 1962a).

Sampath (1962) recently re-examined the inter-relationships of Oryza species and proposed a number of revisions in taxonomy. On the basis of differences in morphology, geographical distribution and genetic affinity with O. sativa, the O. perennis complex was separated into two species: the African O. barthii and the Asian O. perennis. These two species were considered to be the most primitive of the genus (Richharia 1960, Sampath 1962). Theoretical considerations of speciation in the genus and the relationships of the species were also discussed by Sampath (1962).

On the basis of comparative chromosome morphology and meiotic pairing in an O. sativa x O. australiensis hybrid; Shastry and Ranga Rao (1961) postulated that O. australiensis appeared to be the most primitive species in the genus.

The mechanisms involved in the speciation of Oryza species have been postulated to include a series of mutations and structural differentiation in the chromosomes. Sampath (1962) conceived that macro- or systemic mutations have played a role in bringing about parallel variation between African and Asian species. Hu (1960) postulated that a series of gene mutations, rather than gross chromosomal changes, have contributed to species differentiation. Oka (1964) hypothesized that mutations and deficiencies at one or other of the duplicated loci had produced inter-sterile groups among and within species. Shastry and co-workers (Shastry and Mohan Rao 1961, Shastry and Ranga Rao 1961, Shastry 1964b) suggested that structural differentiation of chromosomes at varietal and specific levels and desynapsis and timing imbalance at the level of higher taxa have contributed to interspecific hybrid sterility and genetic differentiation.

Genome Analysis

Genome analysis based on chromosome pairing in $F_1$ plants of interspecific crosses has been conducted by Japanese, Indian, Chinese, American, and Belgian workers. Prior to 1960, most of the successful crosses involved species within the section Sativa Roschev. A summary of genome designations proposed by various workers is given in Table 2.

Table 2. Genome designations of Oryza species

| Species | Morinaga & Kuriyama (1960) | Richharia (1960) | Yeh & Henderson (1961a, 1962) | Bouharmont (1962a) |
|---|---|---|---|---|
| O. sativa | AA | $P^2P^2$ | $A_1A_1$ | AA |
| O. sativa var. fatua | - | - | $A_1A_1$ | AA |
| O. sativa var. formosana | - | - | $A_1A_1$ | - |
| O. sativa f. spontanea | AA | - | - | - |
| O. perennis | AA | $P^1P^1$ | - | - |
| O. perennis subsp. balunga | - | - | $A_1A_1$ | - |
| O. perennis subsp. cubensis | AA | - | $A_2A_2$ | - |
| O. perennis subsp. barthii | - | - | A?A? | - |
| O. glaberrima | AA | $P^3P^3$ | EE | $A_1A_1$ |
| O. breviligulata | AA | $P^3P^3$ | EE | $A_1A_1$ |

Table 2. (Cont'd.)

| Species | Morinaga & Kuriyama (1960) | Richharia (1960) | Yeh & Henderson (1961a, 1962) | Bouharmont (1962a) |
|---|---|---|---|---|
| O. stapfii | AA[1] | $P^3P^3$ | EE | $A_1A_1$ |
| O. australiensis | Not AA, BB or CC; EE[2] | - | - | - |
| O. officinalis | CC | $O^1O^1$ | - | OO |
| O. latifolia | CCDD | $O^1O^1O^2O^2$ | - | CCDD |
| O. paraguaiensis | CCDD | - | - | - |
| O. alta | CCDD[1] | $O^1O^1O^2O^2$ | - | OOEE |
| O. minuta | BBCC | $O^1O^1M^1M^1$ | - | BBCC |
| O. eichingeri | BBCC | - | - | - |
| O. malampuzhaensis | - | $O^1O^1O^3O^3$ | - | - |
| O. brachyantha | FF[2] | - | - | - |
| O. schweinfurthiana | - | - | - | FFGG[3] |

[1] Designated by Kihara, Nezu, Katayama, Matsumura, and Mabuchi (1961).

[2] Designated by Li, Weng, Chen, and Wang (1961), and Li, Chen, Weng, and Wuu (1963).

[3] Genomes of F and G could be identical with B, C or D (Bouharmont 1962a).

On the basis of regular metaphase pairing in the $F_1$ hybrids, the Japanese workers (Morinaga and Kuriyama 1960, Nezu et al. 1960) assigned genome A to the three Asian taxa, O. sativa, O. sativa f. spontanea and O. perennis, and to the three African species, O. glaberrima, O. breviligulata, and O. stapfii; whereas Yeh and Henderson (1961a, 1962) and Bouharmont (1962a) observed meiotic irregularities and high sterility in hybrids of the two geographical groups. Yeh and Henderson (1961a) proposed an E genome for the three African species. This discrepancy in observation could be ascribed to the different strains being used and to the differential effects of environmental factors upon pairing behavior. Yeh and Henderson (1961a, 1961b) observed basically normal chromosome pairing and high seed fertility

in hybrids of O. sativa with the three Asian wild forms, O. sativa v. fatua, O. sativa v. formosana and O. perennis subsp. balunga. Meanwhile, chromosome irregularities and high sterility were observed in hybrids of O. sativa with O. perennis subsp. cubensis (American form) and with O. perennis subsp. barthii (African form), hybrid of O. sativa v. formosana with O. perennis subsp. cubensis, hybrid of O. perennis subsp. balunga with O. perennis subsp. cubensis, and hybrid of O. perennis subsp. cubensis with O. perennis subsp. barthii. On the basis of the above evidence, Yeh and Henderson (1961a, 1962) proposed the designation $A_1$ for the genome of O. sativa, O. sativa v. fatua, O. sativa v. formosana and O. perennis subsp. balunga; $A_2$ for O. perennis subsp. cubensis; and $A_?$ for O. perennis subsp. barthii. On the other hand, the Indian workers suggested the use of the genome symbol P to indicate O. perennis as the archetype of the group involving O. perennis, O. sativa, O. glaberrima, O. breviligulata and O. stapfii; letter O to represent the genome of O. officinalis and its related tetraploid species; and M to indicate an unidentified genome in O. minuta. The superscripts were added to indicate chromosome differentiation among related species (cf. Richharia 1960).

Bouharmont's studies (1962a) indicated that the genomes of O. sativa, and of O. officinalis and O. schweinfurthiana were sufficiently structurally differentiated to warrant the assignment of the genome symbols AA, OO and FFGG respectively. Bouharmont ascribed the meiotic irregularities and sterility observed in some O. sativa x O. glaberrima and O. sativa x O. stapfii hybrids to translocations and to physiological disturbances by genotypic factors.

Structural differences between the chromosomes of O. sativa and those of O. glaberrima were also indicated in three other studies. In a hybrid between tetraploid O. sativa and tetraploid O. glaberrima, Hinata and Oka (1962c) observed a mean frequency of four quadrivalents. In amphidiploids of O. glaberrima x O. sativa and O. sativa x O. breviligulata, Richharia and Govindaswami (1963) and Gopalakrishnan et al. (1964) reported that modes of six, eight, and ten quadrivalents were most frequently found at meiosis.

Most rice cytogeneticists agree that O. officinalis has a genome, C or O, which is distinct from that of O. sativa, A. Morinaga and co-workers postulated that the C genome of O. officinalis is present in the tetraploid species, O. eichingeri, O. latifolia, O. minuta, and O. paraguaiensis (cf. Morinaga and Kuriyama 1960). Kihara et al. (1961) added the postulate that the C genome is also present in O. alta.

However, there is disagreement concerning the other genome present in the tetraploid species. Nandi (1936, 1938) and Okura (1937) considered that the A genome is present in O. minuta, whereas Morinaga (1940) failed to find bivalent formation in the O. sativa x O. minuta hybrid. Kihara and co-workers reported that in the $F_1$ of O. breviligulata x O. eichingeri, 4 bivalents were frequently observed. In the $F_1$ of O. sativa x O. minuta, 5 bivalents were commonly seen. These suggest that the A genome is partially homologous with the B genome of O. eichingeri and O. minuta (Nezu et al. 1960, Kihara et al. 1961). Li, Weng, Chen and Wang (1962) noted that the $F_1$ of O. sativa x O. latifolia gave as many as 11 bivalents at meiosis, suggesting that the two species have one modified O. sativa genome in common.

Doubling the chromosomes of the O. latifolia x O. minuta hybrids resulted in an increase of pollen sterility from 0% in the sterile hybrids to 50% in the amphidiploids (2n=96). However, the mean frequency of quadrivalents per pollen mother cell in the amphidiploids was found to be two (Morinaga, Kuriyama and Ono 1964). This was rather unexpected since the amphidiploids were supposed to include the CCDD genomes of O. latifolia and the BBCC genomes of O. minuta.

Previous to 1960, viable seeds of interspecific crosses were obtained only from crosses among species of the section Sativa Roschev. Crosses among the three species within the section Coarctata failed to produce any viable $F_1$ seeds (Nezu et al. 1960). With the aid of tissue culture, Li, Weng, Chen and Wang (1961) were able to obtain the first intersectional hybrid from O. paraguaiensis x O. brachyantha. From the crosses of O. australiensis with O. sativa, O. officinalis and O. minuta, the Japanese workers postulated that the genome of O. australiensis is not AA, BB or CC (Nezu et al. 1960, Morinaga, Kuriyama and Murty 1962). On the basis of additional crosses with O. paraguaiensis and O. alta, the Chinese workers designated the genome of O. australiensis as E (Li, Chen, Weng and Wuu 1963) and later as G (Li 1964).

A summary of chromosome pairing and fertility in the above interspecific hybrids is given in Appendix B. The genome designations of reasonably well studied species and subspecies are regrouped below, following those genome symbols recently recommended by the 1963 Symposium on Rice Genetics and Cytogenetics. The superscripts denote subgroups which have basically similar genomes but which also exhibit detectable differences in meiotic behavior and fertility relationships in their

hybrids (cf. Chang 1963).

| Genomes | Species | Distribution |
|---|---|---|
| AA | O. sativa[1], O. sativa v. fatua (or f. spontanea), O. perennis subsp. balunga | Asia |
| $A^bA^b$ | O. perennis subsp. barthii | Africa |
| $A^{cu}A^{cu}$ | O. perennis subsp. cubensis | America |
| $A^gA^g$ | O. glaberrima[1], O. breviligulata, O. stapfii | Africa |
| CC | O. officinalis | Asia |
| BBCC | O. minuta[1], O. eichingeri | Asia, Africa |
| CCDD | O. latifolia[1], O. alta, O. grandiglumis, O. paraguaiensis | America |
| EE | O. australiensis | Australia |
| FF | O. brachyantha | Africa |

[1]Representative species of the sub-group.

The above summary indicates that genome analysis of the species within the section Sativa Roschev. is nearly completed and that new studies are needed for the remaining species.

Recently, Shastry, Sharma and Ranga Rao (1961) have questioned the advisability of relying on conventional criteria in genome analysis, namely, chromosome pairing at diakinesis and metaphase I, differences in chromosome size at these stages, crossability between the two species, and the fertility of the interspecific hybrid. These authors pointed out the usefulness of studying chromosome behavior at the pachytene stage in such investigations. Pachytene analysis in the $F_1$ hybrid of O. sativa x O. officinalis revealed nearly complete pairing between the chromosome complements of the two species; whereas the same hybrid showed a high frequency of univalents at diakinesis and metaphase I, as previously reported by Ramanujam (1937b) and Nandi (1938), probably as a result of desynapsis rather than lack of homology. On the above basis, Shastry, Sharma and Ranga Rao (1961) suggested that the relationship between the two species and the role of O. officinalis in the evolution of

cultivated rice should be re-examined. However, recent studies by Li and co-workers (cf. Li 1964) failed to substantiate the above postulate of homology between the chromosome complements of the two species at pachytene and early diplotene.

In the $F_1$ of O. sativa x O. australiensis, comparative studies of chromosome behavior at prophase, diakinesis and meta-anaphase I suggested that the chromosomes from O. australiensis condensed and migrated early to the poles. This timing difference was conceived by Shastry and Ranga Rao (1961) as one of the important factors leading to non-pairing between chromosome complements of the two species and sterility in the hybrid, whereas Li and co-workers (Li 1964) observed allosyndetic bivalents in the prophase stage of the hybrid and therefore ascribed the differential condensation of the chromosomes to the different amount of heterochromatin present in the two complements.

The above contrasts in experimental results and interpretations point to the need for a wider sampling of plant material to adequately represent the diversity of strains within Oryza species, the desirability of exchanging experimental material among workers, the necessity of studying both prophase and metaphase pairings, the need for uniformity in describing meiotic phenomena, and the need to differentiate genes controlling pairing in different genomes and the genomes themselves. Amphidiploidy and backcrossing appear to be two convenient tools for resolving some of the problems in genome analysis.

## The Origin and Indigenous Centers of Cultivated Rices

### Putative Ancestors of Oryza sativa

A number of hypotheses regarding the putative ancestors of O. sativa are summarized in Table 3.

Table 3. Putative ancestors of O. sativa and their center of origin.

| Progenitors | Center of origin | Authors |
|---|---|---|
| O. fatua<br>O. officinalis | South India<br>South India | Watt (1891) |
| O. fatua | South India | de Candolle (1896) |

Table 3 (cont'd.)

| Progenitors | Center of origin | Authors |
|---|---|---|
| O. sativa f. spontanea | Southeast Asia | Roschevicz (1931) |
| O. minuta | Asia | |
| O. officinalis | Asia | |
| O. sativa v. fatua | India and Southeast Asia | Ramiah and Ghose (1951) |
| O. perennis | India, Ceylon, S. America, and Africa | |
| O. perennis | Southeast Asia | Sampath and Rao (1951) |
| O. sativa v. fatua | India, Indo-China and China | Chatterjee (1951) |
| O. officinalis | India and Burma | |
| O. perennis | Asia | Morishima, Oka and Chang (1961) |
| O. balunga (O. perennis subsp. balunga) | Asia | Yeh and Henderson (1961b) |

Roschevicz (1931) suggested that whereas the center of diversity of O. sativa is in India, the center of origin of the section Sativa Roschev. is in Africa. Roschevicz shared the view of his predecessors that O. sativa was derived from a number of species within the section Sativa; i.e., it was polyphyletic in origin. Recent evidence from cytogenetical studies of interspecific hybrids indicates that O. sativa had a monophyletic origin.

In recent years, the question of the putative progenitor of O. sativa has narrowed to three hypotheses.

(1) O. sativa f. spontanea as the ancestral species

O. sativa f. spontanea Roschev., also known as O. fatua Koenig or O. sativa var. fatua Prain, includes a large group of wild annual plants found in the subtropical and tropical marshy lands of Asia (Bor 1960). Great variability is present in this group. There are neither precise morphological differences to separate spontanea from the cultivated form nor genetic barriers to gene exchange between the two populations. Populations of spontanea freely hybridizing with cultivated varieties have been found in Taiwan (Oka 1956b). Another population has been located in Ceylon (cf. Richharia 1960). Roschevicz (1931), Hamada (1949), Zukovskij (1950), Chatterjee

(1951), and Pórteres (1956) suggested that O. sativa f. spontanea is most likely the progenitor of O. sativa in view of their similarity in various characters.

(2) O. perennis as the ancestral species

O. perennis Moench is a perennial grass often found in deep-water swamps. It is a complex comprised of 3 geographical subspecies or varieties: the strongly rhizomatous subspecies barthii of Africa, the weakly rhizomatous and erect subspecies cubensis of the West Indies, and the floating subspecies balunga of Asia (Chatterjee 1951, Sampath and Govindaswami 1958, Richharia 1960). Wide variations in several characters are observed in this complex. As used in genetic literature, O. perennis occasionally included O. sativa f. spontanea (Oka and Chang 1960, Morishima, Oka and Chang 1961).

Asian O. perennis and O. sativa f. spontanea have the same chromosome number (2n = 24) and their hybrids are fertile to varying degrees. Both forms cross readily with O. sativa and the hybrids are fertile and normal in chromosome pairing. Thus, they both may be considered as genetically close to O. sativa and as the progenitors of O. sativa (Ramiah and Ghose 1951, Sampath and Rao 1951). Tateoka (1962a, 1962b, 1963) has grouped the two forms into one species, O. rufipogon Griff.

However, O. perennis subsp. balunga and O. sativa f. spontanea appear well differentiated in the mode of adaptation to habitat, as evidenced by differences in propagating habit (vegetative propagation vs. seeds). Populations intermediate between perennis and spontanea tend to approach the cultivated type (Morishima, Oka and Chang 1961).

Studies of the spontanea forms of wild rice in Orissa, India, revealed their heterozygous nature and hybrid origin (Sampath and Govindaswami 1958). Progenies resembling spontanea were observed in a cross between an Indian variety of O. sativa and O. perennis subsp. balunga (Sampath and Rao 1951, Sampath and Govindaswami 1958, Richharia 1960). The Indian workers maintained that the introgressive hybridization of O. sativa by Asian strains of O. perennis has contributed to the origin of O. sativa f. spontanea (Richharia 1960, Sampath and Seetharaman 1962). The large amount of genetic variability detected in O. perennis populations indicates their potentiality to give rise to different forms when released (Morishima, Oka and Chang 1961). Samples of wild and cultivated forms from the Jeypore Tract of Orissa State, gave a continuous array of intergrades connecting the perennis forms with culti-

vated varieties. Those approaching the wild forms were the perennis type and could be considered as a bridge connecting wild forms with cultivated varieties (Oka and Chang 1962). Thus, O. perennis of Asia may be conceived as the progenitor of both O. sativa f. spontanea and O. sativa (Sampath and Rao 1951, Richharia 1960, Morishima, Oka and Chang 1961, Oka and Chang 1962, Sampath 1962).

In view of the high fertility of crosses between O. sativa and O. perennis subsp. balunga and the regular meiotic pairing in the hybrid, Yeh and Henderson (1961a, 1961b) supported the proposal of Sampath and Govindaswami (1958) that O. sativa was derived from O. perennis subsp. balunga through intermediate forms resembling O. sativa var. fatua or O. sativa var. formosana and that the current forms of fatua arose through natural hybridization between sativa and the earlier types of fatua. Henderson (1963) also suggested the name Oryza x rufipogon Griff. for the annual fatua hybrids of relatively recent origin.

Oka and his associates postulated that in the course of evolution the O. perennis type of wild rice had changed from the vegetative habit of propagation to seed propagation, high incidence of out-crossing to self-pollination, and long period of seed dormancy to shorter periods. Meanwhile, recessive mutations or deletions at those duplicate loci controlling gametophytic and sporophytic fertility had produced inter-sterile groups (Hinata and Oka 1962a, 1962b; Oka 1964).

(3) O. officinalis as an ancestral species

On the basis of morphological features, Watt (1891), Roschevicz (1931) and Chatterjee (1951) suggested that O. officinalis might have played a role in the evolution of cultivated rice. Anderson (1951) also pointed out the introgression of O. officinalis into cultivated forms. The nearly complete pachytene pairing observed in the O. sativa x O. officinalis hybrid by Shastry, Sharma and Ranga Rao (1961) led these workers to reconsider the contribution of O. officinalis to the evolution of cultivated rice.

Among the above hypotheses, the consideration of the Asian O. sativa f. spontanea being an ancestral form is losing favor among American, Chinese, Indian, and Japanese workers who envisage the Asian form of O. perennis as a more likely progenitor (Sampath and Rao 1951, Richharia 1960, Yeh and Henderson 1961a,

Oka and Chang 1962, Sampath 1962, Korah 1963), whereas Shastry, Sharma and Ranga Rao (1961) have re-opened the probable role of O. officinalis in the evolution of O. sativa.

Indigenous Center of Oryza sativa

Archaeological evidence found in India dates the antiquity of rice to 1,000 B.C. (Chatterjee 1951). Similar discoveries from China indicate that rice was being grown in north-central China about 2,800 B.C. (Roschevicz 1931, Chatterjee 1951). Recorded history points to 3,000 B.C. (Ting 1949). Rice cultivation probably began about ten thousand years ago. It appears that upland culture preceded lowland culture (Hamada 1949).

The generally accepted origin of O. sativa is the area embracing South Asia, Southeast Asia, and China (Watt 1891, Roschevicz 1931, Hamada 1949, Ramiah and Ghose 1951, Chatterjee 1951, Morinaga 1955). Cultivated rice spread from India to Egypt early in the Christian era and later to Europe, Africa, the Americas, and Australia. From China, it spread to Korea and Japan. As few specimens of wild forms were found on the mainland of China, China was not considered by several workers as a primary center of origin (Zukovskij 1950, Ramiah and Ghose 1951, Richharia 1960). Other workers held that China is one of the centers (Roschevicz 1931, Ting 1949, Chatterjee 1951) and that the differentiation of the japonica varieties took place in China (Chou 1948, Ting 1949, Morinaga 1955, Morinaga 1956). Specimens of rice glumes found in the Yangtze River in red burned clay belonging to the Neolithic era were identified as the kêng (japonica) type of O. sativa f. spontanea which resembled the cultivated varieties grown today in eastern China (Ting 1960).

On the basis of morphological features and fertility in $F_1$ hybrids, the japonica varieties of China and Japan and the bulu varieties of Indonesia are considered by Japanese workers to be derivatives of the aus type of the Indian subcontinent; the indica varieties of China and the tjereh varieties of Indonesia, as the derivatives of the aman type in India and Pakistan (Morinaga 1955, Morinaga and Kuriyama 1955, Morinaga 1956, Nakao 1957, Morinaga and Kuriyama 1958). On the other hand, Sampath and Seetharaman (1962) regarded the japonica varieties as derivatives of hybrids between indica varieties and Asian O. perennis strains present in south China and Taiwan.

Indigenous Center of Oryza glaberrima

O. glaberrima has its primary center of variation in the central Niger delta of West Africa and probably originated around 1,500 B.C. There are two other secondary centers in Africa (Portéres 1956). According to Chevalier (1932) and Portéres (1956), O. glaberrima is a cultivated form of O. breviligulata. The hybrid between the two species showed normal chromosome pairing and high fertility (Morinaga and Kuriyama 1960, Nezu et al. 1960, Yeh and Henderson 1962). A continuous array of intergrades between populations of O. breviligulata and O. glaberrima was observed (Morishima, Hinata and Oka 1963). Oka and his coworkers (cf. Oka 1964) suggested that O. breviligulata and O. perennis had a common ancestor. On the other hand, Indian workers held that O. perennis is the probable ancestral species (Sampath and Rao 1951, Richharia 1960) and that O. breviligulata corresponds to the intermediate spontanea type in O. sativa. It has been suggested that the differentiation of the two cultivated species, O. sativa and O. glaberrima, has resulted from small chromosomal rearrangements followed by a series of parallel mutations from a common ancestral type, a form of O. perennis (Richharia and Seetharaman 1962). Portéres (1956) postulated that O. glaberrima and O. sativa were derived from a common ancestral form which had rhizomes, floating growth habit and alternate racemes on the panicle. However, this primitive form was not necessarily O. perennis.

Rice workers agree that O. sativa and O. glaberrima have independent geographic origins (Portéres 1956, Kihara 1959, Richharia 1960, Morishima, Hinata and Oka 1962b, Yeh and Henderson 1961a, Sampath 1962, Seetharaman 1962). It appears that O. sativa is of earlier origin than O. glaberrima (Portéres 1956, Kihara 1959, Seetharaman 1962).

## Cytological and Cytogenetical Studies

### Chromosome Morphology

Investigations by Pathak (1940) indicated that the 24 chromosomes of O. sativa were distributed as 8 median and 16 sub-median or sub-terminal chromosomes.

A study of the somatic cells in haploid plants of two O. sativa varieties, Norin 8 and Takara, showed that on the basis of the centromere position the 12 chromosomes were divisible into three groups: 4 median, 5 sub-median and 3 sub-

terminal ones. Two of the sub-terminal chromosomes have satellites (Hu 1958a). In another haploid plant of Norin 8, 4 median, 6 sub-median and 2 sub-terminal chromosomes were reported (Ishii and Mitsukuri 1960). In a haploid plant of Taichung 65, the chromosomes were distributed as 3 median, 7 sub-median and 2 sub-terminal (Hu 1964). A similar karyotype was observed in haploid plants of O. glaberrima (Hu 1960).

Pachytene analysis in variety Norin 6 of O. sativa indicated that the 12 bivalent chromosomes were distributed as follows: 2 median, 8 sub-median and 2 sub-telocentric chromosomes. Two nucleoli were often observed. The ratios between the short and long arms of each chromosome were given (Shastry, Ranga Rao and Misra 1960). Ishii and Mitsukuri (1960) reported that in diploid Norin 8, 3 median, 8 sub-median and 1 telocentric chromosome pairs were observed in root-tip cells. Sen (1963) reported that the 12 chromosomes of an indica variety at pachytene and at pollen mitosis were distributed as 2 median, 9 sub-median and 1 sub-telocentric. Varieties differed considerably in chromosome length and morphology (Korah 1963). Comparison of various studies on chromosome length and position of centromere in O. sativa is given by Hu (1964).

The pachytene chromosomes of O. australiensis were marked by distinct centromeres and a high degree of heterochromatization (Shastry et al. 1960, Shastry and Mohan Rao 1961, Shastry and Ranga Rao 1961). The karyotypes of O. perennis and O. officinalis showed seriation of dense chromomeres. The chromosomes of O. sativa and O. glaberrima also exhibited a seriation of micro- and macro-chromomeres occasionally interrupted by short, densely stained segments.

Shastry and Mohan Rao (1961) studied the karyomorphology of O. australiensis, O. glaberrima and O. stapfii at the pachytene stage. The twelve chromosomes of all the three species were identifiable by the length, arm ratios and chromomeric pattern. A comparison of the karyotypic symmetry of a number of wild and cultivated species is given by Shastry (1964a). In general, the wild species exhibited more symmetrical karyotypes than the cultivated species (Korah 1963, Shastry 1964a). The japonica varieties of O. sativa appeared to be more asymmetric in their karyotypes than the indica varieties (Shastry 1964a).

Many workers agree that the basic chromosome number of the genus is five (Sakai 1935, Nandi 1936, Parthasarathy 1938a, Ramanujam 1938, Okuno 1944, Shama Rao and Seetharaman 1955, Ishii and Mitsukuri 1960, Shastry and Mohan Rao 1961).

Secondary Association of Chromosomes

Early observations by Kuwada (1910), Sakai (1935) and Nandi (1936) indicated a tendency of chromosomes to be associated during meiosis of normal diploid plants. Occasional quadrivalent association was observed at diakinesis and metaphase, and secondary association of bivalents at metaphase I or of univalents at metaphase II. Similar associations were observed in some haploid and triploid plants of O. sativa (Ichijima 1934, Ramanujam 1937a, Hu 1957) and other diploid species of Oryza (Hu 1962). These observations, together with the findings of duplicate genes (Chao 1928a, Mitra and Ganguli 1932, Oka 1953, Oka 1957a, Ramirez et al. 1960), led to the hypothesis that O. sativa originated through hybridization of two divergent 5-chromosome species, in which two chromosomes were duplicated, followed by a doubling of the chromosomes. Thus, the 12-chromosome set of rice may be represented by abcde, a'b'c'd'e' and a"b" (Sakai 1935, Nandi 1936, Takenaka et al. 1956). Similar patterns of secondary associations were observed in six other diploid species (Hu 1962). However, this theory of secondary association and morphological resemblances between chromosomes is not accepted by all other rice workers (Morinaga and Fukushima 1934, Hirayoshi 1957, Shastry et al. 1960, Bouharmont 1962b).

The number of nucleoli in pollen mother cells of different varieties was once studied intensively as a means to differentiate the indica varieties from the japonica (Selim 1930, Nandi 1936, Sakai 1938, Parthasarathy 1938a, Oka 1944, Kuang 1951, Oka and Kao 1956, Shinohara 1962) and to support the hypothesis of secondary chromosome association (Gates 1937, Parthasarathy 1938a, Ramanujam 1938). The nucleolar number varied from one to two in the pollen mother cells and from two to four in the somatic tissues. The size of the nucleoli also showed considerable variability among varieties and at different meiotic stages. No critical evidence related to the above objectives is noted.

Haploids, Polyploids and Aneuploids

Haploid plants have occurred spontaneously in nature, in X-rayed progenies, or in the progenies of hybrids. The haploid plants were reduced in size of every part in varying proportions. Even the number of tillers, number of spikelets, panicle length and pollen mother cells were affected. Haploids were completely sterile, unless pollinated by normal pollen from diploid plants. The meiotic behavior of haploids has been described by Morinaga and Fukushima (1934) and Hu (1957).

Autotriploid plants have been found in nature (Ramiah and Rao 1953) and from irradiated progenies (Nishimura 1957, Katayama 1963a). Allotriploid plants were obtained with difficulty by crossing a diploid with a tetraploid (Ramanujam 1937a, Nandi 1938, Shama Rao and Seetharaman 1955, Morinaga 1964, Nagamatsu, Omura and Koga 1964). The autotriploid plant was generally more vigorous than the diploid, producing broad leaves, stout tillers and large floral parts. The fertility of triploid plants was generally low (0-24%). Cytological observations of triploids have been reported by Ichijima (1934), Morinaga and Fukushima (1935), Ramanujam (1937a), and by Hu and Ho (1963). Cells with 10 trivalents were most frequently observed. Pairing between non-homologous chromosomes was also reported.

Autotetraploid plants also have occurred spontaneously (Morinaga and Fukushima 1937). Many other tetraploids have been produced by colchicine and temperature treatments (Beachell and Jones 1945, Cua 1952, Oka 1954, Bouharmont 1961) or by irradiation (Katayama 1963a). Tetraploids also showed gigas effects as did triploids, but could be distinguished from the latter by their reduced plant stature, short rachis and reduced number of spikelets per panicle. The fertility of tetraploid plants was generally low. Descriptions of meiosis in tetraploid plants are given by Morinaga and Fukushima (1937), Oka, Hsieh and Huang (1954), and Bouharmont (1963). Hybrids between autotetraploids showed relatively normal chromosome behavior and heterosis (Oka, Hsieh and Huang 1954, Oka 1954, Oka 1955a). Gene segregation in autotetraploids was discussed by Morinaga and Kuriyama (1949), Morinaga (1951), and Oka (1955a). Autotetraploid plants appeared to be more tolerant to gamma radiation than their diploid forms in terms of both growth inhibition and mutation rate (Yamaguchi and Ando 1959).

Aneuploids including monosomics and polysomics have been reported (Ichijima 1934, Ramanujam 1937a, Jones and Longley 1941, Sampath and Krishnaswamy 1948, Seshu and Venkataswamy 1958). Aneuploids of 2n + x types have been obtained by crossing a triploids with diploid (Ramanujam 1937a, Katayama 1963b) or by irradiation (Nagamatsu 1955, Nishimura 1957). Trisomic plants were also obtained from the progenies of partly sterile plants (Jones 1952) or of asynaptic plants (Katayama 1963b). Sterility, low viability and abnormal meiotic behavior were common in aneuploids.

Aberrant Meiotic Behavior

Asynaptic plants have been found in nature and among X-rayed progenies. Meiosis in the microsporocytes of the asynaptic plant is characterized by the complete failure of homologous chromosomes to synapse at prophase or metaphase and the presence of univalents leading to irregular distribution of chromosomes at the first anaphase. The frequency of chiasmata per bivalent was reduced. Splitting of univalents, presence of lagging chromosomes, and supernumery spindles were also observed. Such irregular behavior resultd in the complete abortion of pollen grains and eggs.

The asynaptic plants were marked by highly steri le panicles (Ramanujam and Parthasarathy 1935, Jones and Longley 1941, Katayama 1961). The asynaptic behavior was either inherited as a single recessive gene (Nishimura 1957, Katayama 1961), or controlled by either one of two duplicate recessive genes (cf. Ghose et al. 1960).

A mutant showing desynapsis was isolated from irradiated material. Normal synapsis was observed at early prophase. The separation of chromosomes occurred at diplotene, and varying numbers of univalents were observed at diakinesis and metaphase. High seed sterility in desynaptic plants was inherited as a single recessive gene (Chao and Chai 1961). Desynaptic behavior was enhanced or induced by low temperatures during gametogenesis (Nagai 1958, Chao and Hu 1961).

Chromosome Aberrations

Chromosome aberrations have appeared either spontaneously or as a product of artificial induction. Only a few cases of spontaneous aberrants have been described in rice. The aberrants were detected because of their sterility or mor-

phological abnormality or both. In sterile diploid plants of the variety Caloro, partial asynapsis and univalents were observed at meiosis (Jones and Longley 1941). In semi-sterile plants described by Terao (1921) and Miyazawa (1935), semi-steriles gave progenies in the ratio of 1 fertile: 1 semi-sterile. These appear to be a case of chromosomal interchange, although the Japanese workers ascribed the semi-sterility to gene mutation and lethal action of gametes.

Among induced mutants, chromosomal aberrations in the form of univalents, quadrivalents, fragments, asynapsis, syncyte formation, laggards, thick spindles, knot formation, persistent nucleoli, and bridges were usually observed (Parthasarathy 1938a, Nagamatsu 1955, Nishimura 1957, Ouang and Chang 1958, Bora and Rao 1958, Huang and Chang 1958, Korah 1958, Shastry and Ramaiah 1961, Shah et al. 1961, Katayama 1963a, Venkatanadha Chari 1963a). Chromosome interchanges appearing as semi-steriles comprised the most commonly detected type of aberration.

In plants carrying chromosome interchanges, quadrivalent formations (rings or chains), "pairs" of bivalents, rod- or ring-shaped bivalents, and occasionally other configurations were observed. In the ring-type configuration both 'open' (adjacent) and 'zigzag' (alternate) forms were observed with similar frequency (Huang and Chang 1958; Hsieh, Chang and Young 1959; Soriano 1959, 1960, 1961a; Hsieh 1961b). In plants containing a ring of six chromosomes or two rings of four chromosomes, pollen fertility was low (Huang and Chang 1958).

Reciprocal translocation homozygotes were isolated by test-crosses between fertile progenies of translocation heterozygotes and the untreated original variety (Nishimura and Kurakami 1952, Oka, Chang and Huang 1953, Chang 1955, Huang and Chang 1958, Hsieh et al. 1959). Such translocation homozygotes did not differ markedly in phenotypic appearance from their original strain and appeared homogeneous in various agronomic traits (Hsieh et al. 1962).

Inter-crosses between reciprocal translocation homozygotes would yield information on the different chromosomes involved in various translocation lines (Nishimura 1961, Hsieh 1961b). By treating single translocation homozygotes with X-rays, followed by test crosses, double translocation homozygotes have been obtained (Huang 1961).

By crossing translocation lines involving known chromosome segments with testers carrying marker genes, Nishimura (1961) identified the following association between certain gene loci and specific chromosomes: 'short culm'-IV, 'resistance to bacterial blight'- and 'liguleless'-XI, 'tip color of glume'-VI, 'extra glume'-IV, and 'yellow leaf'-V. Trisomics were observed in progenies of translocation heterozygotes of the ring type (Katayama 1963a).

The comparative effects of X-rays, thermal neutrons, beta-particles, and other mutagens on rice seeds and plants have been reported by Nishimura (1957), Matsuo, Yamaguchi and Ando (1958), Yamaguchi (1959), Shah, Beachell and Atkins (1961), Shastry and Ramaiah (1961), Matsuo and Onozawa (1961), Chao and Chai (1961), Horvat (1961), Soriano (1961b), Hsieh (1962), Matsumura and Mabuchi (1962), Kawai (1962a, 1963), and Venkatanadha Chari (1963a).

## Geographical Groups of Cultivated Rices and Intervarietal Hybrid Sterility on Oryza sativa

### Geographical Groups

Working with about 200 varieties, Kato and co-workers (Kato et al. 1928, 1930) proposed to divide O. sativa into two sub-species, japonica and indica, on the basis of morphological differences, serological reactions and sexual affinity. The japonica group included varieties from Japan, Korea and northern China, whereas the indica group consisted of varieties from India, southern China, Taiwan, Ceylon, Java, and other tropical areas. The finding of hybrid sterility between the two groups (66-100% sterility in hybrids as contrasted to 16-51% within japonicas and 29-31% within indicas) aroused much interest among rice workers.

Later studies with larger collections of varieties showed that the morphological variations between the two variety-groups were not discontinuous (Oka 1958), and the phenomenon of intervarietal hybrid sterility was too complicated to allow a classification into two distinct groups (Terao and Mizushima 1939). On the basis of hybrid sterility, eleven groups whose affinity varied from one extremity to the other were recognizable (Mizushima 1948, 1950). The inclusion of a number of bulu varieties from Java (Wagenaar et al. 1952) indicated that they formed a morphologically distinct group (Matsuo 1952). The javanica varieties showed a very high affinity with Japanese varieties and a high to very high affinity with most of the

indica varieties tested (Terao and Mizushima 1944). Thus, three major variety-groups are generally recognized by Japanese workers.

The above three groups and their general morphological features are summarized as follows.

| indica | japonica | javanica |
|---|---|---|
| Broad, light green leaves | Narrow, deep green leaves | Broad, stiff, light green |
| Slender, somewhat flat grains | Short, roundish grains | Broad, thick grains |
| Profuse tillering | Medium tillering | Low tillering |
| Mostly awnless | Awnless to long awned | Awnless or long awned |
| Thin and short hairs on glumes | Dense and long hairs on glumes | Long hairs on glumes |
| Easy shattering | Low shattering | Low shattering |

Information on various agronomic characters of the three variety-groups may be found in papers by Nagamatsu (1943a, 1943b), Ru (1944), Matsuo (1952), Nagamatsu and Ishikawa (1951, 1954) and Oka (1958).

A comparative summary of nomenclature for the variety-groups used by various Japanese workers is given below.

| Kato-Morinaga (cf. Morinaga 1954a) | Terao-Mizushima (1944) | Matsuo (1952) | Oka (1958) | Center of diversity |
|---|---|---|---|---|
| japonica[1] | Group Ia, Ib | Plant type A | Temperate-insular (Group IIb) | Temperate regions |
| indica[1] | Group II, III | Plant type C | Continental (Group Ia, Ib) | Tropical regions |

[1]The ancient Chinese classification of rice into "kêng" and "sên" ( = "hsien"), which predates the Japanese schemes, corresponds to the designation of japonica and indica respectively (Ting 1949). The tjereh varieties of Indonesia and the aman varieties of India and Pakistan belong to the indica type (Morinaga and Kuriyama 1958).

| Kato-Morinaga (cf. Morinaga 1954a) | Terao-Mizushima (1944) | Matsuo (1952) | Oka (1958) | Center of diversity |
|---|---|---|---|---|
| javanica[2] | Group Ic | Plant type B | Tropical-insular (Group IIa, IIb) | Tropical islands (Indonesia) |

[2]The term javanica refers to the bulu varieties from Java (Morinaga 1954a). The bulu varieties of Indonesia and the aus varieties of India and Pakistan, which showed high or fairly high affinity with both indica and japonica groups, are grouped by Japanese workers into the "Intermediate type" (Morinaga and Kuriyama 1958). According to Dutch and Indonesian workers, the bearded bulu varieties are identical with japonica, and the beardless gundil (morphologically similar to bulu except for awnlessness) constitutes a separate group, indo-japonica (Wagenaar et al. 1952). On the other hand, Parthasarathy (1958) considered the bulu varieties to be variants of indica.

The above scheme of dividing rice varieties into geographical races is rapidly losing its significance. Varieties which fall into the japonica group have been isolated in semi-wild conditions from Nepal (Nakao 1957), Ceylon (cf. Richharia 1960), the Jeypore Tract of Orissa, India (Govindaswami and Krishnamurty 1958, Oka et al. 1959), and northern Thailand (Oka and Chang 1963). Hybridization by breeders has further confused the classification scheme. Despite the short-comings, the terms indica and japonica are often used as convenient terms to designate different plant and grain types.

In O. glaberrima, Portéres (1956) reported that there are homologous variations. Two groups, indicoides and japonicoides, could be differentiated in O. glaberrima, corresponding to indica and japonica of O. sativa, respectively. However, Morishima, Hinata and Oka (1962b) failed to find sufficient diversity within O. glaberrima to justify the above differentiation scheme.

Intervarietal Hybrid Sterility in Oryza sativa

Sterility in $F_1$ hybrids of distantly related parents and in their progenies is a common phenomenon. The degree of sterility varies widely in different crosses, ranging from zero to nearly complete sterility.

The general features of hybrid sterility in O. sativa are summarized as follows:

1. The degree of sterility in the $F_1$ is determined by the parents in the cross-combination.
2. In most cases, $F_1$ sterility of reciprocal crosses is not significantly different.
3. Chromosome pairing in micro- and macro-sporocytes is essentially normal, although structural differentiation of chromosomes of various forms in sterile hybrids has been reported; degeneration of the gametes begins shortly following the meiotic divisions.
4. Among the progenies of partly and highly sterile $F_1$'s, segregation for sterility is generally noticeable in subsequent generations; both true-breeding fertile lines and partly sterile lines can be isolated by selection. There is little or no correlation between $F_1$ and $F_2$ sterility; the correlation between $F_2$ and $F_3$ is much higher.

Intervarietal hybrid sterility has been given three interpretations: genic, chromosomal and cytoplasmic. Among the genic hypotheses, Hsu (1945) attributed pollen sterility in two indica-japonica crosses to two complementary genes, one of which was duplicated. However, no true-breeding sterile $F_3$ lines were found. Oka (1953a, 1957a) postulated that in the $F_1$ plants a series of duplicate genes ("gametic-development genes"), whose double-recessive combination ($x_1x_2$) interrupted the post-meiotic development of gametes carrying them, controlled gametic sterility. It was also assumed that several independent sets of duplicate genes were present and that one of the sets was linked with the waxy (*wx*[1]) gene. However, on this basis, sterility should occur only in $F_1$ plants heterozygous for the "gametic-development genes" and fertile plants should produce only fertile progenies. Actually, partly sterile progenies have been found in the $F_2$ and later generations of a highly fertile $F_1$ hybrid, and lines breeding true for sterility have appeared in progenies of partially sterile plants. Later studie

[1] Italic letters refer to gene symbols of the IRC-recommended set (IRC 1959).

by Oka and co-workers showed that highly fertile $F_1$ hybrids segregated widely for sterility, and true-breeding partially sterile lines were obtained. Embryological observations showed that both male and female gametes partly degenerated shortly after normal meiosis during pollen and embryo-sac mitosis (Hsieh and Oka 1958). Oka and Doida (1962) then postulated that duplicate dominant genes ("duplicate-fertility genes") sustained the post-meiotic development of gametes if at least two dominants ($A_1A_1$, $A_2A_2$ or $A_1$-$A_2$-) were present in the plant and that this sporophytically controlled sterility might be due to certain recessive recombinations of these genes.

Examples:

(1) Partial sterility of $F_1$ plants

Parents: $X_1X_1x_2x_2$ and $x_1x_1X_2X_2$

$F_1$: $X_1X_2$, $X_1x_2$ and $x_1X_2$ are viable gametes, and $x_1x_2$ are non-viable gametes.

(2) Partial sterility in $F_2$ and derivatives

Parents: $A_1A_1a_2a_2$ and $a_1a_1A_2A_2$

$F_1$: $A_1a_1A_2a_2$ are fertile plants

$F_2$: $A_1a_1a_2a_2$ or $a_1a_1A_2a_2$ are partially sterile, and $a_1a_1a_2a_2$ breeds true for partial sterility.

Oka (1957b) also postulated a mechanism of dominant lethals to explain the weakness of $F_1$ plants and another of complementary recessive lethals to account for vegetative breakdowns in $F_2$ plants. On the other hand, heterosis in the form of vegetative growth and/or yield increment has been frequently observed in $F_1$ hybrids (Jones 1926, Kadam et al. 1937, Capinpin and Punyasingh 1938, Ramiah and Ramasamy 1941b, Brown 1953, Richharia and Misro 1959) and $F_2$ populations (Mitra 1962).

Jones (1930) first ascribed the sterility in crosses of Chinese and Japanese varieties to "incompatibility in the chromosome mechanism." Terao and Mizushima (1939) and Jones and Longley (1941) considered the sterility between japonica and indica varieties as a result of gene mutations and genic rearrangements within the chromosomes which were accumulated during a long period of separation. Burnham (1956) commented that the phenomena of hybrid sterility observed in diploids and in tetraploids could be explained by chromosomal interchanges. Parthasarathy (1958) postulated that the bulu varieties of Indonesia were derived from indica introductions as stable variants with chromosome rearrangements. Sampath (1960)

suggested that the japonica varieties were differentiated from the indica varieties through a process involving reciprocal translocations followed by mutations at the deficient or duplicated loci.

Cytological investigations by Japanese and Chinese workers showed that meiosis in partially sterile hybrids was essentially normal (Kato et al. 1930, Terao and Mizushima 1939, Liu 1944, Kuang and Tu 1949, Kuang 1951). They suggested that sterility was caused either by lethal effects of genes or minute structural differences in the chromosomes. Cua (1951, 1952), Masima and Uchiyamada (1955a), Masima, Sato and Uchiyamada (1958), and Bouharmont (1961) found that the fertility of partially sterile $F_1$ hybrids was improved by artificial doubling of the chromosomes and concluded that sterility was affected by complex gene mutations and rearrangements within the chromosomes. A lower frequency of quadrivalents and univalents was observed in the tetraploid hybrids than the autotetraploid varieties (Cua 1952, Oka et al. 1954). In one study no significant correlation was found between the frequency of quadrivalents and seed fertility (Oka et al. 1954); whereas, in another study the higher fertility in hybrid tetraploids was ascribed to reduction in the number of quadrivalents (Masima and Uchiyamada 1955b). Mello-Sampayo (1952) found dicentric bridges and acentric fragments at anaphase 1 in a partially sterile hybrid of a cross between two japonica varieties and concluded that the sterility was due to a paracentric inversion. Sampath and Mohanty (1954) found that meiosis in partially sterile hybrids was normal, but bridges with fragments were observed at anaphase I in 11 of the 85 hybrids. These workers assumed that inversions were responsible for the sterility in the 11 hybrids, but in others the sterility was caused by genic or cytoplasmic factors since chromosomal abnormalities were not found. Hsieh (1957) and Hsieh and Oka (1958) observed univalents, 'stretched' chromosomes and anaphase bridges in pollen mother cells of both semi-sterile $F_1$ plants and fertile parents. As the frequencies of occurrence in $F_1$'s and their parents were similar, they concluded that these phenomena were not indicative of the chromosomal differences between distantly related varieties. More recently, Yao, Henderson and Jodon (1958) and Henderson, Yeh and Exner (1959) found two types of abnormal chromosome behavior in intervarietal hybrids: bridges without fragments and bridges with fragments. Bridges without fragments were found in equal frequency in different homozygous varieties and were

therefore considered not abnormal or indicative of structural differences in chromosomes. Bridges accompanied by fragments were found at very low frequencies in 9 of the 12 hybrids, indicative of paracentric inversions. Shastry and Misra (1961) studied the pachytene chromosomes in japonica x indica hybrids and observed three types of aberrations: heteromorphic bivalents, quadrivalents, and incomplete chromosome pairing, which are indicative of deletions, translocations and differential segments, respectively. A sub-terminal inversion loop was found in a bivalent of one hybrid, suggesting a pericentric inversion. Among the four kinds of abnormalities, loose pairing was by far the most common. The above observations led Shastry and Misra to conclude that indica and japonica groups were differentiated by a series of small structural differences in their chromosome complements and that sterility in the hybrids might be considered as "recombinational" between chromosome segments. However, such loop formation was observed both in parents and their hybrids (Wu et al. 1964), and critical evidence for translocated segments is lacking. On the other hand, Henderson (1964) suggested a possibility in which two inversions within the same chromosome arm were involved, producing adjacent, overlapping and included inversions. This type of included inversion is difficult to detect cytologically, yet it would produce higher sterility than single paracentric inversions. In summary, most rice workers tend to recognize hybrid sterility as a result of cryptic structural differentiation in chromosomes between the two variety-groups (Terao and Mizushima 1939, Jones and Longley 1941, Kuang and Tu 1949, Cua 1952, Morinaga 1954a, Yao et al. 1958, Henderson et al. 1959, Sampath 1960, Shastry and Misra 1961).

Differences in pollen and seed fertility between reciprocal $F_1$ hybrids of Indian and Japanese varieties were noted by Sampath and Mohanty (1954). In two series of reciprocal crosses, lower fertility was observed when a Japanese variety was used as the female parent. Differences in fertility of japonica x indica hybrids backcrossed to different parents were noted by Nagamatsu and Omura (1958). Katsuo and Mizushima (1958), Mizushima (1960), and Hinata and Oka (1962a) have also noted differences in fertility between reciprocal crosses involving O. sativa f. spontanea and cultivated varieties from China, India and Japan. Lower fertility was observed when the wild forms were used as the female parent. Backcrosses of spontanea x cultivated hybrids to cultivated varieties gave lower fertility than backcrosses of the same hybrids to wild forms. The low fertility was ascribed to non-

dehiscent anthers and non-viable pollen. Katsuo and Mizushima suggested that cultivated varieties carried nuclear genes which reacted with the cytoplasm from wild strains to produce sterility. Kitamura (1960, 1962) analyzed similar cases of sterility in hybrids of distantly related parents. He postulated that three types (T, K and M) of cytoplasm were present in Chinese, Philippine, Ceylonese and Vietnamese varieties of the indica type. Interaction between one of the above types of cytoplasm with a "sensitive" nuclear gene in certain Japanese varieties would result in non-dehiscent anthers. High sterility or "sensitivity" appeared to be dominant to low sterility.

It is evident from the above that more extensive and critical studies are needed to elucidate these problems of great importance to breeders.

In actual breeding work, hybrid sterility does not appear to be the most serious obstacle to wide crosses. It has been shown that sterility can be bred out of a segregating population by rigorous selection and fully fertile lines have been obtained (Hsu 1945, Chalam 1959, Caffey 1961). However, the possibility of hybrid sterility restricting segregation and recombination in subsequent generations, as pointed out by Oka (1955, 1956, 1957c), Sampath (1959), and Richharia and Misro (1959), is noteworthy. Experimental evidence on modified segregation ratios and restricted recombination due to gametic and zygotic selection in hybrid progenies has been presented by Oka (1953, 1955b, 1956c, 1957c, 1957d). The effect of environmental factors on the expression of hybrid sterility has been reported by Kuang and Tu (1949), Wagenaar et al. (1952), IRC (1956), Miller (1959), Caffey (1959) and Sampath (1964).

## Genetic Studies

Many simple mutant characters in O. sativa have been described and their mode of inheritance reported. A tabulation by Ramiah and Rao (1953) listed 58 spontaneous mutants and 38 artificially induced mutants. A 1959 International Rice Commission summary (IRC 1959) listed 90 mutant traits for which the mode of inheritance is known. Additional tabulations are given in two 1963 IRC reports (Anon. 1963, Chang and Jodon 1963).

### Genes for Color

Pigmentation of the various parts of the rice plant involves a most fascinating and complicated system of gene interaction. Anthocyanin pigmentation

varies in intensity and distribution. It is found in all of the vegetative parts and several floral parts but not in the embryo or endosperm. The color of the apiculus is useful in analyzing the inheritance of pigmentation, not only in the apiculus itself but also in other vegetative organs. Thus, the genes for apiculus color are also basic for anthocyanin formation in other organs (Nagao 1951), although several exceptions have been noted (Jones 1929, Ramiah 1945, Misro et al. 1960).

Two complementary series of alleles, C[1] and A, determine anthocyanin formation. C is the basic gene for the production of chromogen, and A (previously known as Sp) controls the conversion of chromogen into anthocyanin. C and A are genes with multiple allelic series: 6 alleles have been determined for C and 4 for A. The order of dominance is given below (Nagao et al. 1962).

$$C^{B} > C^{Bp} > C^{Bt} > C^{Br} > C^{Bm} > C^{+} \text{ or } c$$

$$A^{E} > A > A^{d} > A^{+} \text{ or } a$$

In addition, five other genes control the distribution of anthocyanin in Japanese varieties: P (previously designated as A) controls the spreading of chromogen over the entirety of the apiculus; Pr (Rp) controls the color over the glumes and rachilla; Pl with 3 alleles (Pl, $Pl^{W}$ and $Pl^{+}$) governs the pigment distribution over the leaf blade, leaf sheath, pulvinus, auricle, ligule, internode, node, and rachis; Pn conditions the color in leaf apex, leaf margin, stem node, pulvinus, auricle, and ligule; and Ps conditions the localization of pigments in the stigma (Takahashi 1957, Nagao et al. 1962). An inhibitor gene, I-Pl, suppressed the effect of Pl (Kadam 1936b, Nagao et al. 1962, Kondo 1963a). Similarly, other inhibitor genes have been reported for colored apiculus (I-P), colored leaf apex (I-Pla) and colored midrib (Kondo 1963a, 1963b). Through the interaction of the above genes, various color expressions and intensities are possible. Color development is further complicated by the fading and leaching of certain colors. Some red colors disappear by maturity (Nagao 1951, Jodon 1955, Takahashi 1957).

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[1]Italic letters refer to gene symbols of the IRC-recommended set (IRC 1959, Anon. 1963, Chang and Jodon 1963).

The complexity of the pigmentation patterns as conditioned by the interaction of the above genes is illustrated below (Takahashi 1957, Nagao et al. 1962).

(1) Color of apiculus

| Genotype | Color shade at flowering | Color shade at ripening |
|---|---|---|
| $C^{B}$ A P | Blackish red purple | Faded purple |
| $C^{Bp}$ A P | Pansy purple | Faded red purple |
| $C^{Bt}$ A P | Tyrian rose | Faded pink |
| $C^{Br}$ A P | Rose red | Straw white |
| $C^{Bm}$ $A^{E}$ P | Faint red | White or almost white |
| $C^{+}$ A P | White | Straw white |
| $C^{B}$ $A^{d}$ P | Amaranth purple | Tawny |
| $C^{Bp}$ $A^{d}$ P | Pomegranate purple | Light tawny |
| $C^{Bt}$ $A^{d}$ P or $C^{Br}$ $A^{d}$ P | Seashell pink | Yellowish white or white |
| $C^{+}$ $A^{d}$ P | White | White |
| $C^{B}$ $A^{+}$ P | White | Russet |
| $C^{Bp}$ $A^{+}$ P | White | Tawny |
| $C^{Bt}$ $A^{+}$ P | White | Ochraceous-buff |
| $C^{Br}$ $A^{+}$ P | White | Warm-buff |
| $C^{+}$ $A^{+}$ P | White | Straw white |

(2) Color of lemma and palea

| | | |
|---|---|---|
| $C^{B}$ A Pr | Blackish red-purple | |
| $C^{Bp}$ A Pr | Pansy purple | |
| $C^{B}$ $A^{d}$ Pr | Amaranth purple | Tawny |
| $C^{Bp}$ $A^{d}$ Pr | Pomegranate purple | Light tawny |
| $C^{B}$ $A^{+}$ Pr | Green | Russet |
| $C^{Bp}$ $A^{+}$ Pr | Green | Tawny |

(3) Color of leaf blade

| Genotype | Color shade at flowering |
|---|---|
| $C^B$ A Pl or<br>$C^{Bp}$ A Pl | Purple leaf |
| $C^B$ $A^d$ Pl or<br>$C^{Bp}$ $A^d$ Pl | Reddish green leaf |
| $C^{Bt}$ A Pl | Green leaf with pink tint around pulvinus and node |

(4) Color of leaf margin, node and pulvinus

| | |
|---|---|
| $C^B$ A Pn or<br>$C^{Bp}$ A Pn | Purple node and pulvinus with colored leaf margin |
| $C^B$ $A^d$ Pn or<br>$C^{Bp}$ $A^d$ Pn | Red node and pulvinus, the red disappearing in the leaf margin |

The color components in the apiculus, internodes, stigmas and pericarp were identified as chrysanthemin, keracyanin, cyanin and uliginosin (Nagai et al. 1960, 1962; Mizushima et al. 1963). A discussion of the specific action of the various A and C alleles in controlling the production of the above pigments is given by Mizushima, Kondo and Konno (1963).

Other genes which control the distribution or localization of anthocyanin pigments are: (1) Pau, purple auricles, basic to Plg, (2) Pg, purple outer glumes, (3) Pin, purple internode, (4) Pla, purple leaf apex, (5) Plg, purple ligule, (6) Prp, purple pericarp,(7) Psh, purple sheath, (8) Pu, purple pulvinus, (9) Px, purple axil, and (10) Pw, purple-wash of leaf blade (Anon. 1963).

The inheritance studies of anthocyanin pigmentation in plant organs conducted in India have been summarized by Ramiah and Rao (1953) and Ghose, Ghatge and Subrahmanyan (1960). Ramiah and Rao (1953) concluded that two basic genes, A and C, controlled pigments in plant organs. Besides these, there are also genes for intensifying or diluting the pigments and for producing various color

patterns. Hence, two to seven genes are probably involved in the production of different types of pigmentation in the various organs as shown below.

| Plant organ | Probable number of genes |
|---|---|
| 1. Leaf sheath | 5 |
| 2. Leaf blade | 3 to 6 |
| 3. Internode | 3 to 5 |
| 4. Junctura | 2 |
| 5. Leaf axil | 2 to 4 |
| 6. Ligule | 3 to 4 |
| 7. Auricles | 2 |
| 8. Pulvinus | 2 |
| 9. Septum | 2 |
| 10. Outer glumes | 2 to 5 |
| 11. Lemma and palea | 4 to 5 |
| 12. Apiculus | 4 to 5 |
| 13. Stigma | 5 to 7 |
| 14. Awn | 3 |

Kadam of India postulated that a total of eleven genes accounted for all the color segregations that occurred in three crosses (cf. Jodon 1955). However, the applicability of the C-A-P[1] complementary gene system in pigment formation among tropical varieties has been confirmed by Kondo (1963a) and Ghose et al. (1963).

Goldhull was inherited as a simple recessive, gh; white hull, a single dominant, Wh. The $H^m$, $H^i$, $H^g$ and $H^f$ alleles in the presence of Gh controlled other non-anthocyanin colors. Brown furrows on glumes were controlled by a dominant, Bf; black hull by complementary genes, Bh (cf. Anon. 1963).

Red pericarp (red rice) in Japanese varieties was controlled by two complementary genes, Rc and Rd; speckled gray-brown pericarp by Rc. Rd and A were closely linked (Nagao 1951). Reddish brown pericarp was also controlled by the pleiotropic effect of the purple leaf allele, $Pl^w$, when it co-existed with C

[1] P, when used as the first letter of a symbol, denotes anthocyanin color in a certain plant organ or organs; exceptions: Ph, Pl.

in the absence of A (Nagao et al. 1962). The inheritance of purple, red, brown, golden,and grey brown pericarp colors in Indian varieties has been described by Ramiah and Rao (1953). Purple pericarp appeared to be controlled either by Prp or by the pleiotropic effect of the purple leaf gene, Pl or $Pl^W$, in the presence of C and A (Nagao et al. 1962). In other crosses, purple pericarp appeared to be governed by two complementary genes (Hsieh and Chang 1962, Nagai et al. 1962).

Genes for Modified Structures, Sizes and Growth Habit

Several types of dwarfs have been recorded. Most of these were characterized by shortened internodes and undersized grains. Dwarfs were generally single-gene recessives (d), but independent genes ($d_1$, $d_2$, $d_3$. . .) were involved in different types (Jones 1933, Nagao 1951). Among $F_2$ progenies of dwarf x dwarf crosses, double recessives appearing as double dwarfs were obtained (Akemine 1925, Jodon and Beachell 1943); in other cases, intermediate types were obtained (Hsieh 1962). In one case, the dwarf character was inherited as a single dominant (Sugimoto 1923). In other case, a profuse tillering dwarf was controlled by any two of three recessive genes (Butany et al. 1959). A morphological study of several types of dwarfs with special reference to internode elongation has been described by Nagamatsu et al. (1961).

Other dwarfs with long grains, slender culms and narrow leaves have been found (Jodon 1955). Dwarfs with intermediate stature, normal panicle and grains are fairly common in irradiated material (Shah et al. 1961, Huang 1961).

The floating habit of deep-water rice was conditioned by two duplicate recessives, $dw_1$ and $dw_2$. One of the duplicate genes appeared to be linked with a dominant gene for late maturity (Ramiah and Ramaswami 1941a). The production of tillers and roots at higher nodes permits stem elongation as the water rises.

The lazy or ageotropic growth habit was inherited as a single recessive, la (Jones and Adair 1938, Ramiah and Rao 1953). In other instances, the erect habit (er) was recessive to spreading (cf. Anon. 1963).

Extra glumes (lmx), long empty glumes (g) and multiple pistils (mp) were controlled by single recessives (Jones 1933, Nagao 1951, Jodon 1957). In one study, long glumes were controlled by two duplicate recessives, $g_1$ and $g_2$ (Chao 1928a).

The inheritance of awns (An) involves several genetic postulates. Jones (1927, 1933) and Chao (1928a) reported that fully awned and awnless differed by two genes; awnless and partly awned by one gene. In Japanese varieties three genes, $An_1$, $An_2$, and $An_3$, controlled various degrees of awning (Nagao and Takahashi 1942). In Chinese varieties, $F_2$ ratios of 3:1, 9:7 and 15:1 have been reported (Kuang et al. 1946). Others reported that a polygenic system involving major and minor genes appeared more logical (Misro et al. 1961). Awn development could be affected by season, root pruning and level of polyploidy (Sahadevan 1959). A dominant inhibitor for awning (I-An) has been reported (Misro and Misro 1954).

A single recessive gene (lg) controlled the absence of ligule, collar (junctura) and auricle in one study (Jones 1933). In another study, the appearance of each of these characters was controlled by one of three sets of quadruplicate genes ($Au_1 \ldots Au_4$, $Lg_1 \ldots Lg_4$, $J_1 \ldots J_4$). Close linkage between these three sets of genes was observed (Ghose et al. 1957).

Glabrous or smooth hulls in American and Indian varieties were controlled by a single recessive gene (gl); so was glabrous leaf (Ramiah and Rao 1953, Jodon 1955). Glabrous hulls and leaves were usually associated (Misro 1960, Takahashi 1964). In Japanese varieties, in addition to gl, two complementary genes, $Hl_a$ and $Hl_b$, controlled long pubescence of leaves; another gene Hg controlled long pubescence on floral glumes and also affected pubescence on leaf margins, auricles and rachises (Nagao et al. 1960). Smooth hull is a desirable trait in rice that is mechanically harvested, dried and milled (Jodon 1955).

Inheritance of grain shedding or shattering is another unsettled problem. In certain crosses, shattering (Sh) was dominant over non-shattering (Kadam 1936a, Morinaga 1940, Hara 1942); in other crosses, difficult threshing (Th) was dominant over easy threshing (Jones 1933). A polygenic interpretation appears more plausible (Sakai and Niles 1957, Takahashi 1964). The shedding character is associated with the relative degree of development of the abscission layer between the spikelet and the pedicel. Shedding appeared to be inversely associated with the thickness of cell walls in the abscission layer (cf. Nagai 1958).

Tough dehulling (Tf) was reported to be dominant over easy dehulling (cf. Anon. 1963).

Clustering of spikelets (Cl) was inherited as a single gene lacking dominance. Neck-leaf (nl), triangular hull (tri) and 'Sathi' panicle (enclosed by sheaths, ex) were controlled by single recessives (cf. Jodon 1955).

Dense or compact panicle has been reported to behave as a monogenic dominant (Dn) over lax or normal panicle (cf. Anon. 1963). Lax panicles (Lx) were reported to be dominant over compact or normal panicles in other studies (cf. Anon. 1963). In other cases, $F_2$ ratios of 9:7, with the dense panicle either dominant or recessive, have been obtained (cf. Ghose et al. 1960). Spreading panicle branches (spr) behaved as a recessive to the non-spreading type (cf. Anon. 1963).

Round or short spikelet (Rk) has been reported to be dominant over the long oval type (Ramiah and Rao 1953), involving one gene (Chao 1928a) or as many as four complementary genes (Kadam and D'Cruz 1960). A large grain mutant behaved as a simple recessive to the normal (cf. Ramiah and Rao 1953). Another large grain, semi-sterile mutant was also inherited as a single recessive (cf. Nagai 1958). Wide and continuous variations in grain dimensions suggest that grain size and shape are complex quantitative traits.

Sterility of various types has been reported. Reports of sterility due to morphological abnormalities in reproductive or non-reproductive organs of the spikelets have been summarized by Nagai (1958) and Ghose, Ghatge and Subrahmanyan (1960). Most of the abnormalities in reproductive organs were inherited as simple recessives.

Genetic information on other morphological mutants of academic interest were given by Kuang (1951), Nagao (1951), Ramiah and Rao (1953), Jodon (1955, 1957), Nagai (1958), and Ghose, Ghatge and Subrahmanyan (1960). Comprehensive summaries of inheritance studies made in China (Taiwan), India, Japan, Pakistan and the U.S.A. were given in two recent IRC reports (Anon. 1963, Chang and Jodon 1963).

Genes for Modified Composition or Physiological Processes

Nine types of chlorophyll deficiency have been described (Ramiah and Ramanujam 1935). Albinism is generally controlled by a single recessive (al) and is lethal in seedlings. Xantha or yellow (y) seedlings was controlled by a single recessive or two complementary recessives. Chlorina (chl) or yellow-green was

conditioned by a single recessive or two complementary recessives; this trait appears later in the growing period than does xantha. Variegation of leaves in the form of fine- or white-striped leaves is generally controlled by a single recessive (fs or ws), but other non-heritable cases are also known. Other types are virescent yellow (v), lutescent seedlings (lu) and zebras (z), each of which was controlled by a simple Mendelian recessive (Nagao 1951, Ramiah and Rao 1953, Jodon 1955). Five types of lethal chlorophyll deficiencies were reported by Kadam (1941), each involving a single gene or duplicate genes.

Non-pathogenic leaf spots, also known as physiologic leaf spots, appeared to be controlled by single recessives, bl and others (Jodon 1955; Takahashi 1964).

Inheritance of scented or aromatic grains (Sk) depended on one, two or three complementary genes (cf. Anon. 1963); fragrance at blooming was due to a single dominant, Fgr (Jodon 1944).

Brittle stem, leaves and panicles were controlled by one recessive gene, bc (Jones 1933). The brittleness was caused by low α-cellulose content in cell walls (Takahashi 1964).

Dark-violet staining of grains and hulls with phenol solution was inherited as a single dominant, Ph. This staining reaction is usually found in the indica varieties (Nagao 1951).

Glutinous or waxy endosperm, comprised largely of amylopectin, is contrasted with the non-glutinous type containing both amylopectin and amylose; these starch fractions stain brown and blue with iodine-potassium iodide solution respectively. The waxy type of starch is found only in the endosperm and the pollen grains. The non-waxy type is present in the leaves, sheath, roots, culm, embryo, pollen, and endosperm (Watabe and Umekage 1959). Waxy endosperm or pollen is governed by a single recessive gene, wx (gl). Since the endosperm is triploid in constitution, four genotypes can be expected in $F_2$ seeds of a waxy x non-waxy cross and its reciprocal: Wx Wx Wx, Wx Wx wx, wx wx Wx and wx wx wx. Spectro-photometric and iodine color tests have shown that the blue-staining reaction of the Wx allele is not completely dominant but additive (Sugawara 1953, Nagai 1958). In pure varieties, the proportion of amylopectin to amylose appears

to be the same in the endosperm of diploid and tetraploid plants (Watabe and Umekage 1959). In reciprocal crosses between Russia 71 and Kuro-mochi, Shibuya (1962) obtained a 1 non-waxy: 1 waxy ratio in the $F_2$ seeds, indicating that the Gl (Wx) allele in Russia 71 is incompletely dominant over gl (wx) in Kuro-mochi and that the Gl Gl gl genotype yields non-waxy endosperm and the Gl gl gl genotype yields waxy endosperm. The early heading $F_2$ plants produced a higher proportion of non-waxy pollen than the late heading ones. In Aikoku-mochi, Enomoto (1929) reported a mutation of the wx allele to the dominant Wx in the pollen grains at a frequency of 0.104 per cent. There are also lines which have the chalky, opaque endosperm, indicative of the waxy type, and which stains blue with iodine solution (Seetharaman 1964).

In non-waxy x waxy hybrids, there is often a deficiency of the waxy types in the $F_2$ due to a deficiency of pollen carrying the recessive gene (Chao 1928b) or to the lower fertilization rate of the waxy pollen (Oka 1953b, Mizushima and Kondo 1961). The genetic mechanism causing the partial gametic non-functionality has been suggested as either due to the complementary lethal action of two recessive genes, one of which is linked with the wx gene, or to a deficiency of genes in the $F_1$ as a result of structural hybridity (Mizushima and Kondo 1962). In a cross involving an irradiated non-waxy strain and a waxy linkage tester, abnormal segregation for waxy endosperm and apiculus coloration has been interpreted as the action of a gametophyte factor, ga, linked with wx and C. The data suggest that most cultivated glutinous varieties have the dominant allele, Ga, which enhances the functional capacity of the male gemetophytes (pollen grains) carrying Ga (Iwata, Nagamatsu and Omura 1964). Yamaguchi (1963) obtained similar results in crosses involving Japanese upland varieties and suggested that in certain crosses the waxy allele was linked with a sterility gene located in the first linkage group. In wx x Wx crosses, the xenia effect of the non-waxy pollen upon the endosperm of the waxy female parent has been reported (Beachell et al. 1938).

In earlier investigations, resistance to the blast fungus (Piricularia oryzae) was reported to be controlled by one or two dominant genes, $Pi_1$ and $Pi_2$ (Sasaki 1923, Nakatomi 1926, Ramiah and Ramaswami 1936, Hashioka 1950). In one cross, a single recessive gene for resistance appeared to be involved (Ramiah and Ramaswamy 1936). Okada and Maeda (1956) reported that three genes with additive effects were probably involved in controlling resistance to leaf blast. Oka

and Lin (1957) postulated that in a japonica x indica hybrid resistance was controlled by one recessive gene which appeared to be linked with the "gametic-development genes" and the phenol-reaction gene (Ph). Niizeki (1960) reported that two independent genes controlled resistance to two strains of the blast fungus, respectively. Recent studies by Hsieh, Chien and Hwang (1961) and Hsieh (1961c) indicated that two independent genes controlled leaf resistance to several races of the pathogen, while a third gene controlled neck resistance to blast. Yamasaki and Kiyosawa (1962) studied the reaction of several $F_2$ populations to each of seven Japanese races and reported that three dominant genes ($Pi_1$, $Pi_2$ and $Pi_3$) controlled resistance to the fungus. These workers also postulated that different races of the pathogen carried different genes for pathogenicity. In another recent study, Venkataswamy (1963) reported that one dominant gene governed resistance to U.S. blast races 6, 8 and 16. However, reaction to each race was influenced by a different set of modifying genes. In addition to the genes for resistance, an inhibitor gene (I-Pi) or gene for susceptibility has been suggested by Abumiya (1959).

Disease reaction to single physiologic races of Cercospora oryzae was ascribed to single (Ce) or duplicate genes for resistance (Jodon et al. 1944).

In one study, resistance to Helminthosporium oryzae was controlled by one dominant gene, He (Nagai and Hara 1930). In other studies, a wide range of variation in disease reaction was observed in the $F_2$, suggesting that several genes were involved (Atkins and Jodon 1963).

Resistance to Corticium sasakii or Sclerotium oryzae appeared to be controlled by one dominant gene, Sc (TARI 1948, Hashioka 1951).

Resistance to Xanthomonas oryzae was inherited as a single dominant, Xe (Nishimura and Sakaguchi 1959).

Resistance to the hoja blanca virus appeared to be conditioned by one dominant gene (Beachell and Jennings 1961).

Resistance to stem-borers appeared to be dominant over susceptibility and was governed by one or a few genes (Koshairy et al. 1957, Van and Goh 1959, Richharia 1961).

Plant reaction to stem maggots (Chlorops oryzae) appeared to be controlled by a single gene which lacked dominance (Fuke and Koyama 1955, Fukuda and Inoue 1962).

From a cross involving Somewake and Aomori 5, Toriyama (1962) postulated that from 5 to 7 independent genes with additive effect controlled plant tolerance to low air temperatures during the period between panicle formation and flowering. Some of the genes conditioning tolerance showed linkage relationship with the Pr gene in the Pl linkage group and others with one of the An genes. These linkages facilitated selection for tolerance in segregating generations.

Late maturity or sensitivity to photoperiod generally has been observed to be the effect of one completely or partially dominant gene, Lf or Se (Nomura and Yamazaki 1927, Ramiah 1933, Jones et al. 1935, Sethi et al. 1938). The Se locus appeared to involve a series of multiple alleles located on the wx - C linkage group. The Se locus was found to be associated with high tillering ability (Chandraratna 1955). In certain other crosses, sensitivity appeared to be recessive, ef (Sampath and Seshu 1961). Multiple factor inheritance for this trait has been suggested (Ramiah 1933, Sethi et al. 1938), involving two or more loci (Jones 1933, Yu and Yao 1958, Yao and Yu 1963, Chandraratna 1963). The complicating effect of temperature response in such studies has been pointed out by Sampath and Seshu (1961), Chandraratna (1963), and Venkataraman (1964).

Straw strength has been described on the basis of anatomical and structural differences (Ramiah and Dharmalingam 1934, Matsuo 1952, Bollich 1963, IRRI 1964). Plant characteristics which contribute to lodging resistance are short plant stature, short basal internodes near ground level, erect growth habit, thick and cylindrical culm, high culm density, erect and narrow leaves, persistent and tight-wrapping leafsheaths, and high breaking strength of culm. The lodging types are generally associated with tall stature, long basal internodes, broad and drooping leaves, loose leafsheaths, asymmetrical culm section and low breaking strength (IRRI 1964). In several crosses, the $F_2$ ratio was 3 lodging: 1 non-lodging (Ramiah and Dharmalingam 1934, Matsuo et al. 1960, Ramaswamy and Ponnaiya 1963). It was also observed that in two crosses, stiff straw (ld) was linked with poor tillering and late maturity (Ramiah and Dharmalingam 1934). Judging from the complexity of plant characters involved in straw strength, a polygenic hypothesis appeares more logical.

Pollen sterility has been interpreted on the basis of a single recessive gene, s (Ishikawa 1927, Ramanujam 1935) or duplicate recessive genes in the case

of an asynaptic line (Ramanujam and Parthasarathy 1935, Ramiah and Rao 1953). Sterility in partially sterile lines was interpreted on a monogenic (Terao 1921) or digenic basis (Ishikawa 1927). Percent of viable pollen in normally fertile lines could also be lowered by adverse environmental conditions. Some of the known factors are low air and water temperatures, high humidity or excessive rain at flowering, low light intensity, short photoperiod, drought, and nitrogen fertilization (Akemine and Hoshika 1939, Kuang and Tu 1949, Ramiah and Rao 1953, Nagai 1958, Misra 1962). Between pollen and egg sterility, higher incidence of pollen sterility was observed in cases of adverse environments (Nagai 1958), hybrids of distant parents (Yao et al. 1958, Miller 1959, Richharia and Misro 1959, Yamaguchi 1963) or chromosome interchanges (Carpena and Ramirez 1960). Experiments in China, India, Japan and U.S.A. indicated that spikelet sterility often exceeded pollen sterility in intervarietal hybrids and their progenies (Terao and Mizushima 1939, Hsu 1945, Kuang and Tu 1949, Cua 1952, IRC 1956, Hsieh and Oka 1958, Yao et al. 1958, Miller 1959, Richharia and Misro 1959, Oka and Doida 1962, Yamaguchi 1963, Sampath 1964).

Strong seed dormancy appeared to be controlled by two genes, $Sd_1$ and $Sd_2$; high permeability of testa to water by another gene Sg (Takahashi 1962). In other studies, seed dormancy appeared to be a dominant trait governed by a number of genes (Shanmugasundaram 1953, Narayanan Namboodiri and Ponnaiya 1963).

High amylose content as indicated by the iodine test appeared to be controlled by one major gene and several modifiers. Partial dominance was indicated in the $F_1$. The heritability value was estimated at 98 per cent, indicating that amylose content is a highly heritable trait (Seetharaman 1959).

Protein content varies considerably among varieties, ranging from a mean of 7 per cent among many Indian varieties to a mean of 11 per cent in certain U. S. varieties (Sampath and Seshu 1957). Several Hungarian varieties contained 13 per cent crude protein (Lozsa 1951). Sampath and Seshu (1957) found higher protein content (9.4-11.3%) in long glumed varieties and even higher percentage (10.7-13.3%) in autotetraploids. Protein determinations over a number of tests indicated that protein content is a highly variable trait, subject to the influence of envoronmental and nutritional factors (Sturgis, Miears and Walker 1952, Johnston 1961, IRRI 1964). However, progress in selection is attainable (Johnston 1961).

White core (wc or $wb_2$) and abdominal white (wb) of the endosperm appeared to be simply inherited recessives in certain cases (cf. Anon. 1963), or

a dominant character in others (cf. Nagai 1958). A polygenic hypothesis to explain the various types of abdominal white has been offered by Seetharaman (1964).

Genes for Quantitative Characters

Quantitative inheritance in rice in relation to its economic importance has not received enough attention. Matsuura (1933) listed length of grain, length of panicle, compactness of spikelets on the panicle, height of plant, width of leaf, diameter of stem and grain yield as quantitative characters controlled by multiple genes. In addition to these, the breadth and thickness of grain, semi-sterility of spikelets, tillering and seed dormancy were considered by Indian workers to be controlled by polygenes (Ghose et al. 1960).

Syakudo and co-workers (Syakudo and Kobori 1958; Syakudo et al. 1952, 1953, 1954, 1957; Kawase 1961) found that in a number of crosses studied, in addition to a basic gene-complex C, three major genes with measurable effects ($E_1$, $E_2$, $E_3$) governed stem height, panicle length, panicle weight, grain length and maturity. In all, 6 genes for panicle length, 4 for culm length, 4 for grain dimensions and 4 for heading date were detected. From the above studies, the following inferences concerning the action of genes on character development were drawn: (1) There were complementary genes with different direction and intensity in the development of the same character, (2) There was the common phenomenon of interaction among genes, (3) A majority of the genes were pleiotropic, and (4) Significant gene-environment interactions were involved (Kawase 1961).

The number of genes controlling spikelet length has been reported to vary from one dominant (Chao 1928a, Ramiah and Rao 1953) or a recessive (cf. Ramiah and Rao 1953) for short grain to five or more genes (Jones et al. 1935, Morinaga et al. 1943); for grain width, one gene to multiple genes (Jones et al. 1935). Grain length and width appeared to be correlated in certain cases (Ramiah and Parthasarathy 1933, Iyama et al. 1959) but not in others (cf. Nagai 1958). The expression of spikelet and caryopsis dimensions is also subject to the influence of nutritional and environmental factors (Ramiah and Parthasarathy 1933, Iyama et al. 1959, Samoto and Ouchi 1962).

Fuke (1955a, 1955b, 1955c) reported that six genes (Z, M, K, G, O and F) controlled the maturity of late-ripening Japanese varieties, i.e., late varieties contained all six genes. Medium-maturing varieties had five and early ones

four. Plants with K, Z and M genes were sensitive to photoperiod, whereas plants with G, O and F were sensitive to temperature differences. The gene K appeared to be linked with the gene for red apiculus. The complementary action of K and F genes made the plants carrying them highly sensitive to long photoperiod. The genes M and O were linked. It is obvious from the above that earliness or lateness is a composite character greatly influenced by the prevalent growth and cultural conditions, such as time of planting, spacing, manuring and the climatic conditions. The significant effect of photoperiod is reflected in its influence upon photoperiod-sensitive individuals. Therefore, the growth duration of a genotype should be recognized as being comprised of 3 components: basic vegetative growth duration, photoperiod sensitivity, and thermosensitivity. Only when the components are individually studied is it possible to separate the effect of each component (cf. Matsuo 1952, Morinaga 1954b, Chandraratna 1955, Nagai 1958). Isogenic lines, or sister lines breeding true for most other characters, appear well suited for testing the effects of gene differences for maturity.

Sakai and Niles (1957) reported that 3 genes governed plant height, 11 controlled panicle length, and 2 and 6 genes controlled grain shedding in two different crosses.

The estimated heritability values for 5 agronomic characters in an indica x japonica cross were given by Oka (1956a) as: heading date, 0.823; panicle number per plant, 0.090; plant height, 0.317; panicle length, 0.237; grain number per panicle, 0.302. Ru and Kung (1963) also gave estimates for 4 traits in 2 j x i crosses.

Bollich (1957) reported that two or more genes controlled spikelet length; three to five genes governed spikelet width with narrow floret partially dominant over broad floret; both qualitative and quantitative genes controlled heading date with earliness dominant over lateness. The heritability values were given as: (1) spikelet length, 0.86 for $F_2$ data and 0.67 for $F_3$ data; (2) spikelet width, 0.58 for $F_2$ data and 0.64 for $F_3$ data; and (3) heading data, 0.63. The correlation coefficients between $F_2$ and $F_3$ values for spikelet length and width were 0.72 and 0.71, respectively; that for the heading date based on $F_3$ and $F_4$ lines was 0.88. Yield had a low heritability value. The correlation of heading date and yield in this study was estimated at -0.61.

Toriyama and Futsuhara (1958) reported that estimated heritability values were higher for heading date and culm height than for panicle length, panicle number and panicle weight. Ouang and Chang (1958) also reported higher heritability estimates for heading date and plant height than for tiller number in crosses involving irradiated progenies and their parents.

In a cross involving two Ceylonese varieties, Chandraratna and Sakai (1960) estimated that ten genes of additive nature controlled grain weight. Values of 0.769 and 0.401 were given for estimates of gross genetic variance and additive genetic variance, respectively. Maternal effect on grain weight, observed in the $F_1$ and $F_2$ generations, was estimated to be 32 per cent of the total variance.

Nei (1960) reported that in two hybrid populations studied, the heritability estimates for heading date and culm length were higher than those for grain yield, panicle length and number of panicles per plant. Discussions of different methods of estimating the heritability of individual traits, the estimation of coheritability of trait-pairs, genetic and phenotypic correlations and genetic gain, and the usefulness of the selection index were also presented by Nei.

A recent study involving a short non-dwarf variety (105 cm.) and a medium tall variety (129 cm.) indicated that the two parents differed in plant height by two to four "effective factor pairs." Two pairs appeared to be probable when the factors did not give equal contributions to height. If equal increments in height were assumed, four pairs appeared more probable (Mohamed and Hanna 1964).

Inheritance studies of pubescence, apiculus and stigma color, hull color, and glume length in O. glaberrima were reported by Richharia and Seetharaman (1962). Contrasting types in each of the above traits were governed by a single pair of alleles.

Gene Symbols

The use of gene symbols for various characters in rice has been a matter of individual preference. Over 300 genes affecting about 50 plant characters have been recognized. Kadam and Ramiah (1943) proposed certain rules for the symbolization of genes in rice and listed recommended symbols. Their symbolization was followed by workers in India and U.S.A., but geneticists in Japan developed a different set of symbols for the same or similar genes (Nagao 1951). The need

for a uniform set of symbols and a standard system of nomenclature was later recognized by the International Rice Commission of the Food and Agriculture Organization of the United Nations. A working committee consisting of N. E. Jodon, M. E. Takahashi and S. Seetharaman was organized to study the problem and suggest remedial measures. Following the rules of the International Committee on Gene Symbols and Nomenclature, a list of gene symbols was proposed by the IRC committee. Genetic symbols recommended by the committee were adopted by the International Rice Commission and published in the IRC Newsletter (IRC 1959). This was followed by a full report including complete tabulations of recommended and original symbols, citations and literature lists. The summary report was published by the U.S.Department of Agriculture in 1963 (Anon. 1963).

A list of gene symbols under the above three schemes of nomenclature is given in Appendix C. Since 1963, the responsibility of monitoring the gene symbols according to IRC recommendations has been assumed by The International Rice Research Institute and the first attempt at monitoring has appeared in the IRC Newsletter (Chang and Jodon 1963).

Linkage Groups

As O. sativa has 12 pairs of chromosomes, it is expected to possess 12 linkage groups. Present data are still insufficient to fully establish the 12 linkage groups corresponding to the 12 chromosomes. About 50 genes have been assigned to different linkage groups.

In 1948, Jodon summarized and arranged the known data on linkage into eight groups. Additional information from Indian workers was incorporated in Jodon's 1956 paper. Since then, Nagao and Takahashi (1960, 1963) and Takahashi (1964) have attempted the experimental mapping of 12 linkage groups as shown below and have given recombination values. Some of the groups are represented by only two genes (Figure 2).

Additional information on 15 cases of linkage has been supplied by Richharia, Misro, Butany, and Seetharaman (1960). These are assigned to one group as Psh-Px-Pin-P. Some of the crossover values differed from those previously reported from India.

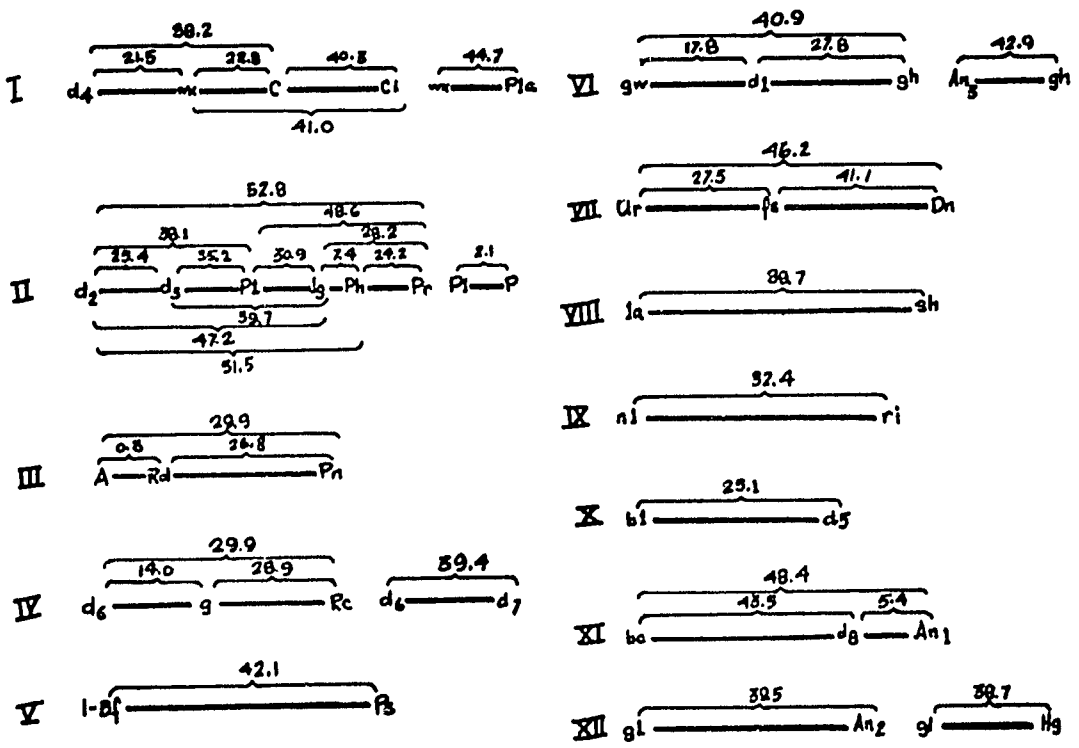


Fig. 2. Trial construction of linkage maps in Japanese rice

Other information on linkage studies has been summarized by Jodon, Takahashi and Seetharaman (Anon. 1963), Nagao and Takahashi (1963) and Jodon (1964).

Recent studies in Japan (Mizushima and Kondo 1959, 1960, 1961, 1962) and India (Richharia et al. 1962, Seetharaman 1964) suggest that the distribution of genes C and A for anthocyanin pigmentation in the various linkage groups of Japanese varieties is different from that in the Indian varieties. Similar anomalous modes of segregation have been reported for characters controlled by wx, Rc, Rd, Cl, lg, and I-Pl (Mizushima and Kondo 1959, 1960, 1961, 1962; Seetharaman 1964). These findings lend support to the theory that cryptic structural hybridity exists in the distantly related varieties of O. sativa. It also appears that complex gene loci are involved in certain cases.

Induced Mutations and Tetraploids

Compared with diploids, tetraploids generally have thicker stems, wider leaves, larger pollen grains, awns, larger seeds, higher sterility, and reduced vigor (Beachell and Jones 1945, Nagamatsu 1954, Richharia 1961). Highly

fertile tetraploid lines have been obtained by selection (Nagamatsu 1954, Richharia 1961), but their agronomic promise remains doubtful.

Induction of mutations has been a popular practice of rice geneticists and breeders since the mid-1930's (Ichijima 1934, Imai 1935, Oryozi 1936, Parthasarathy 1938b). The most common products of induced mutations are chlorophyll deficiencies, dwarfs of varying statures, clustered or lax panicles, delayed or advanced maturity, narrower or broad leaves, narrow stems, awning, lowered fertility, non-shattering spikelets, glabrousness of leaf and hulls, stiffness of culms, changes in grain size and shape, resistance to Cercospora, changes in resistance to Piricularia, and increased genetic variability within populations. For selected references, refer to papers by Nagamatsu (1955), Beachell (1957), Matsuo, Yamaguchi and Ando (1958), Masima and Kawai (1958), Oka, Hayashi and Shiojiri (1958), Bateman (1959), Chang (1960), Lin and Lin (1960), Kao et al. (1960), Hu et al. (1960), Horvat (1961), Li, Hu, Chang and Weng (1961, 1962), Matsuo and Onozawa (1961), Hsieh (1961a, 1962), Kawai et al. (1961), Bekendam (1961), Campos (1962), Chalam et al. (1962), Ota, Sugiyama and Otatani (1962), Yamaguchi (1962), Kawai (1962, 1963), Venkatanadha Chari (1963b), and Yamagata and Syakudo (1963).

In summary, the induction of polyploidy and mutations has been practiced extensively in rice. However, the application of irradiation to assist in the analysis of complex loci, mapping of linkage groups, study of chromosomal interchanges, and interspecific transfer of characters has not been utilized as fully as with other staple cereals.

Cytoplasmic Inheritance

Few cases of cytoplasmic inheritance have been reported in rice. The known ones are the nucleo-cytoplasmic interaction in affecting intervarietal hybrid sterility (Sampath and Mohanty 1954, Katsuo and Mizushima 1958, Mizushima 1960, Kitamura 1960) and the maternal effect on grain weight (Chandraratna and Sakai 1960). The effect of cytoplasmic inheritance on polygenic characters in decreasing genetic variance and reducing the efficiency of selection has been discussed by Chandraratna and Sakai (1960) and Sakai, Iyama and Narise (1961). The inheritance of plastids in variegated plants has been mentioned as a case of cytoplasmic inheritance involving mutable plastids (Katayama and Shida 1951, Pal and Ramanujam 1941, Cho 1955), but little additional information is available on the subject of cytoplasmic inheritance.

## Evaluation of Genetical and Cytogenetical Studies in Relation to Rice Breeding

It can be inferred from the above survey of literature that many of the genetical and cytogenetical investigations of the past were conducted as academic pursuits. Relatively few studies were designed to yield information that would directly benefit rice breeding. The genetic information useful in rice breeding is mainly limited to: (1) knowledge of trait heritability and (2) the mode of inheritance of simple traits, such as pericarp and endosperm characters, glabrousness, growth habit, disease resistance, and pigmentation. The latter aids in the planning of crosses, in the identification of true $F_1$ hybrids from a number of crossed seeds, in estimating adequate population sizes for segregating generations, and in the selection of desired genotypes from heterozygotes. As compared to wheat and corn, the rice breeder has received little support from his fellow geneticists and cytogeneticists (Ramiah and Rao 1953). However, by relying on his ability to match parents and on continued selection for the heritable traits, the breeder has been able to achieve marked success in varietal improvement.

Further progress in rice breeding can come from the combined efforts of the breeder and his colleagues in related disciplines, with geneticists and cytogeneticists playing an important part. The necessity for such concerted efforts has been pointed out, using Taiwan as a case study (Chang 1961).

In this connection, genetical and cytogenetical investigations would be of greater value to breeding if: (1) Greater attention is paid to physiological and quantitative traits of economic importance, (2) Intensive research is conducted to elucidate the nature and mechanism of intervarietal hybrid sterility, (3) A synthesis of cytoplasmic male-sterility is attempted to utilize heterosis, (4) More emphasis is placed on the interspecific transfer of a few desired traits such as disease and insect resistance, and (5) Studies on hybrid populations are made to formulate more efficient selection and breeding systems.

In the realm of interspecific crosses, O. perennis has been suggested as a source of tolerance to water-logging and for improving deep-water rice; O. officinalis as a source for tolerance to deep flood; O. perennis var. longistaminata and O. sativa f. spontanea as gene-pools to provide drought resistance; O. perennis var. cubensis to provide resistance to Helminthosporium oryzae; O. coarctata as a source of resistance to salinity; O. ridleyi from Malaya to provide resistance to stem

borers; and O. glaberrima as a promising source of enhanced adaptability to low soil fertility and of improved grain quality (Ramiah and Ghose 1951, Chalam 1959, Richharia et al. 1961, Richharia and Govindaswami 1962, Morishima et al. 1962a). Moreover, certain wild species would certainly furnish desired resistance of high levels to various rice diseases, if studies are made in this field.

Most of the wild species have certain traits which are considered undesirable in cultivated varieties: extreme shattering habit, long and strong seed dormancy, sensitivity to photoperiod, high incidence of natural cross-pollination, weak straw, perennial growth habit in the case of perennial species, spreading panicles and low response to fertilization (Morinaga and Fukushima 1956, Oka and Chang 1959, Morinaga and Kuriyama 1960, Seetharaman 1962). Many of these undesirable traits are known to be controlled by dominant genes (Mitra and Ganguli 1928, Hara 1942). In one instance, it was shown that introgressed populations of O. sativa f. spontanea with O. sativa gave values intermediate between spontanea and sativa for panicle length, percent of outcrossing, natural shedding of grains, and seed dormancy and in addition showed response to transplanting, weeding, and manuring, whereas grain weight was little affected (Oka and Chang 1959, 1962b). However, it would require a large number of backcrosses and long years of continued selection to recover the various agronomic traits desired in cultivated varieties. Sterility may also become a problem in progenies of interspecific hybrids. It follows that interspecific hybridization between cultivated and wild forms may be attempted only when the breeder fails to find any other available source of desired genes. Great variability is present in existing cultivated varieties, particularly those of tropical origin (Ramiah and Ghose 1951, Govindaswami and Krishnamurthy 1959, Richharia 1961). As much of this variability has not been exploited, it seems advisable for rice breeders to first survey and utilize the existing sources of desired traits.

A collection of 10,000 cultivated varieties has been assembled and is being maintained at The International Rice Research Institute. These varietal stocks are being made available to interested breeders everywhere following appropriate observation, cataloging and seed increase. More diverse germ plasm can be readily added to the above collection if extensive field collections are made in tropical areas where natural variability among native varieties has not been well

sampled previously. According to most rice workers in Asia, collections in northeast India, East Pakistan, Indonesia, the Philippines, Burma, Vietnam, Cambodia, Laos, Thailand, and Borneo would enrich the variability now at hand. Meanwhile, dwindling sources of variability due to wider varietal adaptability and a reduction in the number of cultivated varieties, is creating a need for preserving existing natural sources of germ plasm (Harlan 1956, Myers 1961, Jensen 1962).

Current literature indicates that in recent years, many rice workers have become interested in radiation as a tool in breeding. Although radiation of rice varieties does yield certain desired traits, e.g., reduced plant stature, earlier maturity, and an increased genetic variability within populations, the induction of mutations has not produced any trait of economic importance which is not found in natural populations. Therefore, it seems more advisable to utilize the available natural variability through suitable screening and breeding procedures (Harlan 1956, Myers 1960).

## Areas Requiring New Or Renewed Efforts

It is obvious from the foregoing review that in recent years there has been much interest among rice geneticists and cytogeneticists in the genome analysis of the genus Oryza mainly as a step in studying the origin and speciation of rice. Achievements to date in this area compare favorably with the work on other cereals. The much aroused interest in radiation genetics and breeding is also comparable to that in other crop plants. However, in other areas, notably the inheritance of economic traits of value to breeding, research in rice lags behind that in other cereals. It seems apparent that the total research funds devoted to rice have been less than those allocated to wheat and corn.

At the Symposium on Rice Genetics and Cytogenetics held at The International Rice Research Institute in 1963, the conferees agreed that the following areas merit attention in the future:

1. Extensive genetic analysis of economic traits, especially of physiological and quantitative characters of importance to plant breeders.

2. Development of more complete linkage maps, both in indica and japonica types.

3. Completion of a set of trisomics and a set of translocations within a single japonica variety, within a single indica variety, and within a single "ponlai" variety.

4. Clarification of the nature of intervarietal sterility, using both cytogenetic and genetic approaches, with special emphasis on studies in leptotene, pachytene, and diplotene.

5. Extension of studies of genome analysis to species in sections other than Sativa, which is relatively complete, and the utilization of amphidiploids.

6. Clarification of species relationships still in dispute. Further collections of African material are necessary.

7. Studies on the inheritance of resistance to Piricularia oryzae, to stem borers and to other important diseases and pests.

8. A continuing and thorough search of the world collection of rice varieties for characters of interest to taxonomists, geneticists, and plant breeders.

9. Preservation of genetic material used in important genetic studies, particularly those stocks used as analysers. These might be deposited with IRRI for later use by scientists wishing to verify earlier results or to make comparative genetic studies.

10. Genetic studies of hybrid populations and on the interspecific transfer of desirable traits.

Cooperative efforts in the above fields are needed to attain progress. Such a coordinated approach is being followed at The International Rice Research Institute. Scientists of various disciplines are studying problems which include nitrogen response, photoperiodism, straw strength, disease resistance, insect resistance, and grain quality. On an international basis, cooperative research has been initiated on a number of subjects with institutions in southeast Asia, Taiwan and Japan. It is hoped that the Institute's efforts in sponsoring cooperative research and symposia, and its training program will significantly contribute to the development of cooperative activities among rice scientists of the world.

Some of the cooperative activities made since the 1963 Symposium are (1) the cooperative collection of plant material in Africa with IRRI serving as a germ plasm bank, (2) the extensive exchange of experimental material among workers through IRRI, (3) the appointment of working committees to strive for

uniformity and improvement in taxonomical and genetical nomenclature, and (4) the channeling of genetic information on testers and symbols through IRRI, with the International Rice Commission Newsletter serving as the dissemination channel. It is expected that cooperation will be further intensified when the objectives, activities and services of the Institute reach additional rice workers.

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The author realizes that there are undoubtedly other contributions on rice genetics and cytogenetics which he has not reviewed. He will appreciate it if these are called to his attention, along with any errors which need correcting.

## Appendix A

Synonyms of Oryza Species Under Four Classification Schemes

| Roschevicz (1931) | Chatterjee (1948) | Tateoka (1963) | Sampath (1962) |
|---|---|---|---|
| Sect. Sativa Roschev. | | | |
| australiensis | australiensis | australiensis | australiensis |
| breviligulata | breviligulata | breviligulata | breviligulata |
| glaberrima | glaberrima | glaberrima | glaberrima |
| grandiglumis | grandiglumis | grandiglumis | grandiglumis |
| latifolia | latifolia | latifolia | latifolia |
| longistaminata | perennis (African) | barthii | barthii |
| minuta | minuta | minuta | minuta |
| officinalis | officinalis | officinalis | officinalis |
| punctata | punctata | punctata | punctata |
| sativa | sativa | sativa | sativa |
| sativa f. spontanea | sativa v. fatua | rufipogon | rufipogon |
| Schweinfurthiana | punctata | punctata | eichingeri |
| Stapfii | stapfii | breviligulata | breviligulata |
| | alta | alta | latifolia |
| | eichingeri | eichingeri | eichingeri |
| (Dewildemani)[1] | perennis (African) | barthii | |
| | perennis (Asian and American) | rufipogon | perennis (Asian) |
| | perrieri | perrieri | perrieri |
| | tisseranti | tisseranti | tisseranti |
| Sect. Granulata Roschev. | | | |
| granulata | granulata | meyeriana | granulata |
| Abromeitiana | meyeriana | meyeriana | meyeriana |
| Sect. Coarctata Roschev. | | | |
| brachyantha | brachyantha | brachyantha | brachyantha |
| coarctata | coarctata | coarctata | coarctata |

[1]Roschevizc listed, but did not describe, this species in his Russian text.

| Roschevicz (1931) | Chatterjee (1948) | Tateoka (1963)[1] | Sampath (1962) |
|---|---|---|---|
| Sect. Coarctata Roschev. | | | |
| Ridleyi | ridleyi | ridleyi | ridleyi |
| Schlechteri | schlechteri | schlechteri | schlechteri |
| | | longiglumis | |
| Sect. Rhynchoryza Roschev. | | | |
| subulata | subulata | | subulata |
| | | | ubanghensis |
| | | | malampuzhaensis |
| | | angustifolia | brachyantha subsp.. angustifolia |

[1]Tateoka recently studied the leaf anatomy of 12 taxa and the embryo structure of 18 taxa and proposed (1) to remove O. coarctata from the rest of Oryza and recognize it as Sclerophyllum coarctatum (Roxb.) Griff., and (2) to place O. angustifolia, O. brachyantha, O. longiglumis, O. perrieri, O. ridleyi and O. tisseranti in a new section, Ridleyianae. Thus, the genus Oryza includes 3 sections: Sativae (Oryza), Granulatae, and Ridleyianae (cf. Bot. Gaz. 124: 264-270, 1963; Amer. J. Bot. 51: 539-543, 1964).

## Appendix B

**Chromosome Pairing and Fertility in Interspecific Hybrids**

| Cross[1] | $F_1$ hybrids MI pairing (mode) | Pollen/seed fertility[2] |
|---|---|---|
| 1. 2x x 2x | | |
| O. sativa x O. sativa f. spontanea | 12 II (140, 248, 162)[3] | PF-F (140, 248, 162)[3] |
| O. sativa x O. sativa f. fatua | 12 II (405) | PF-F (405) |
| O. sativa x O. sativa v. formosana | 12 II (405) | PF-F (405) |
| O. sativa x O. perennis | 12 II (140, 210, 248, 162) | PS-F (140, 210, 248, 162) |
| O. sativa x O. perennis v. barthii | 12 II (405) | PS-PF (405) |
| O. sativa x. O. perennis v. cubensis | 12 II (417, 210, 405) | S-F (412, 210, 405) |
| O. sativa x O. balunga | 12 II (405) | PF-F (405) |
| O. sativa x O. glaberrima | 12 II (140, 210, 248) | S (140, 210, 248, 342) |
| O. sativa x. O. glaberrima | 12 II or 2-24 I (406, 17) | PS-S (406, 17) |
| O. sativa x O. breviligulata | 12 II (140, 210, 248, 162) | S-PS (140, 210, 248, 162) |
| O. sativa x O. breviligulata | 12 II or 2-24 I (406) | PS-S (406) |
| O. sativa x. O. stapfii | 12 II (248, 143, 17) | S (248, 17) |
| O. sativa x. O. stapfii | 12 II or 2-24 I (406) | S (406) |
| O. sativa x. O. officinalis | 24 I (245, 295, 210, 248, 357) | S (245, 295, 210, 248, 357) |
| O. sativa x. O. australiensis | 24 I (210, 248, 355) | S (210, 248) |
| O. sativa x O. australiensis | 22 I + 1 II (cf. 156) | |

[1] Author's designation of species name is followed.

[2] Rating of fertility: F (fertile) >70%; PF (partly fertile) 31-70%; PS (partly sterile) 1-30%; S (sterile) 0%.

[3] Italic numbers in parenthesis refer to a list of references following these Appendices.

| Cross | $F_1$ hybrids MI pairing (mode) | Pollen/seed fertility |
|---|---|---|
| O. sativa x O. australiensis | 20 I + 2 II (158) | - |
| O. sativa f. spontanea x O. perennis | 12 II (162) | PF-F (248, 162) |
| O. sativa f. spontanea x O. breviligulata | 12 II (162) | PS (248, 162) |
| O. sativa v. formosana x O. perennis v. cubensis | 12 II (405) | PS (405) |
| O. sativa x O. brachyantha | 24 I (395) | PS-S (395) |
| O. perennis x O. glaberrima | 12 II (248, 143) | PS (248) |
| O. perennis x O. breviligulata | 12 II (162) | S-PS (248, 162) |
| O. perennis v. cubensis x O. perennis v. barthii | 12 II (405) | F-S (405) |
| O. perennis v. cubensis x O. balunga | 12 II (405) | S-PS (405) |
| O. glaberrima x O. balunga | 12 II or 2-4I (406) | S-PS (406) |
| O. glaberrima x O. breviligulata | 12 II (210, 406) | PF-F (210, 248, 406) |
| O. glaberrima x O. stapfii | 12 II (406) | F (406) |
| O. officinalis x O. australiensis | 24 I (248, 143, 212) | S (248) |
| 2. 2x x 4x or 4x x 2x | | |
| O. sativa x O. eichingeri | 36 I (210) | S (210, 248) |
| O. sativa x O. grandiglumis | 36 I (213) | S (213) |
| O. sativa x O. latifolia | 36 I (210) | S (210, 248) |
| O. sativa x O. latifolia | 26I + 5 II (162) | S (162) |
| O. sativa x O. minuta | 10II + 10I + 2III (283) | S (283) |
| O. sativa x O. minuta | 12II + 12I (245) | S (245) |
| O. sativa x O. minuta | 36 I (210., 162) | S-PS (210, 162) |
| O. sativa x O. minuta | 24 I + 6 II (248) | S (248) |
| O. sativa x O. paraguaiensis | 36 I (210, 162) | S (210, 162) |
| O. sativa f. spont. x O. eichingeri | 36 I (162) | S (248, 162) |
| O. sativa x O. schweinfurthiana | 36 I (17) | S (17) |
| O. glaberrima x O. eichingeri | 36 I (210) | S (210) |
| O. glaberrima x O. grandiglumis | 36 I (214) | S (214) |
| O. glaberrima v. grandiglumis x O. eichingeri | 17 I + 5 II + 3 III (348) | S (348) |

| Cross | $F_1$ hybrids MI pairing (mode) | Pollen/seed fertility |
|---|---|---|
| O. glaberrima x O. minuta | 36 I (cf. 156) | S (cf. 156) |
| O. breviligulata x O. eichingeri | 28 I + 4 II (248, 143) | S (248) |
| O. stapfii x O. latifolia | 36 I (248, 143) | S (248) |
| O. officinalis x O. alta | 12 II + 12 I (248, 143) | S (248) |
| O. officinalis x O. grandiglumis | 12 II + 12 I (214) | S (214) |
| O. officinalis x O. latifolia | 12 II + 12 I (210, 316) | PS-S (210, 316) |
| O. officinalis x O. malampuzhaensis | 18 I + 9 II (55) | F (55) |
| O. officinalis x O. minuta | 12 II + 12 I (245, 210) | S (245, 210) |
| O. officinalis x O. paraguaiensis | 12 II + 12 I (210, 162) | S (162) |
| O. australiensis x O. alta | 22 I + 7 II (161) | S (161) |
| O. australiensis x O. minuta | 36 I (213) | S (213) |
| O. australiensis x O. minuta | 28 I + 4 II (158) | PS-S (158) |
| O. australiensis x O. paraguaiensis | 20 I + 8 II (161) | S (161) |
| O. paraguaiensis x O. brachyantha | 36 I (161) | S (161) |
| O. brachyantha x O. minuta | 36 I (395) | PS-S (395) |
| 3. 4x x 4x | | |
| O. grandiglumis x O. paraguaiensis | 24 II (214) | PF (214) |
| O. latifolia x O. alta | 24 II (248, 143) | S-PS (248) |
| O. latifolia x O. grandiglumis | 24 II (142, 214) | S-PS (142, 214) |
| O. latifolia x O. minuta | 12 II + 24 I (210, 162) | S-PS (210, 248, 162) |
| O. latifolia x O. paraguaiensis | 24 II (210) | PS-PF (210, 162) |
| O. malabarensis x O. latifolia | 12 II + 24 I (161) | - |
| O. minuta x O. eichingeri | 24 II (210) | PS (210) |
| O. minuta x O. grandiglumis | 12 II + 24 I (214, 141) | S (214) |
| O. minuta x O. paraguaiensis | 12 II + 24 I (210, 162) | S (210, 162) |

| Cross | $F_1$ hybrids MI pairing (mode) | Pollen/seed fertility |
|---|---|---|
| O. malampuzhaensis x O. latifolia | 12 II + 24 I (141) | - |
| O. sativa (4x) x O. schweinfurthiana | 48 I (17) | S (17) |
| O. sativa (4x) x O. glaberrima (4x) | 4 IV + 16 II (68) | PS-PF (68) |
| 4. Amphidiploids | | |
| O. sativa x O. glaberrima | 10 IV + ? (310) | PF (310) |
| O. sativa x O. glaberrima | 8 IV + ? (416) | PS-F (416) |
| O. sativa x O. breviligulata | 8 IV + ? (416) | PS-F (416) |
| O. latifolia x O. minuta | 2 IV + ? (215) | PF (215) |

## Appendix C

### A Comparative Listing of Three Sets of Gene Symbols

| Character expression | Kadam & Ramiah (1943) | Nagao (1951) | IRC (1959), Anon. (1963), Chang & Jodon (1963) |
|---|---|---|---|
| Anthocyanin activator | A | Sp, $Sp^d$ | A, $A^d$ |
| albino | w | al | al |
| Awned | An | An | An |
| asynaptic sterile | fas | as | as |
| awned sterile | fan | ans | |
| rudimentary auricle | au | au | au |
| Brown awn | anbr | | Ban |
| brittle culm | bc | bc | bc |
| Beaked hull | | | Bd |
| Brown furrow (glumes) | Hf | df | Bf |
| big (coarse) culms | | | bg |
| Blackhull | H-b | Rl | Bh |
| Brown internode | Ntbr | | |
| brownish leaf discoloration | | | bl |
| bent node | | | bn |
| Branching at nodes | | | Br |
| Chromogen (anthocyanin) | C | $C^B$, $C^{Bp}$, $C^{Br}$ | C, $C^B$, $C^{Bp}$, $C^{Bt}$, $C^{Br}$ |
| Enhancer of C | | | En-C |
| Cercospora resistance | Ce | Ce | Ce |
| chlorina (chlorophyll deficiency) | chl | ch | chl |
| Clustered spikelets | Sc or Cl | Cl | Cl |
| Super-clustered spikelets | | | En-Cl |
| complete sterile | fc | cs | |
| cleistogamous spikelets | | | cls |
| claw shaped spikelet | | clh | clw |
| dwarfs (general) | d | d | d |

| Character expression | Kadam & Ramiah (1943) | Nagao (1951) | IRC (1959), Anon. (1963), Chang & Jodon (1963) |
|---|---|---|---|
| double awn | | da | da |
| Dense panicle | | dn | Dn |
| Dense (vs. lax panicle) | | | $Dn_2$ |
| Normal (vs. lax panicle) | | | $Dn_3$ |
| Depressed and under-developed palea | | | Dp |
| desynapsis | | | ds |
| floating habit | ef | fh | dw |
| Early flowering (low photosensitivity) | fl | | Ef |
| Enhancer (intensifier) | | | En- |
| erect growth habit | Er | | er |
| Spreading growth habit | Es | Sg | |
| Exerted panicle | Ex | ex | Ex |
| Fragrant flower | | Fgr | Fgr |
| Flowering period | fl | Fl | |
| fine stripe | | fs | fs |
| female sterile | ffs | fes | |
| long outer glumes | g | lng | g |
| goldhull | H-go | Rg | gh |
| glabrous leaf | lh | go | gl |
| Long glume, epistatic to g | | | Gm |
| green-and-yellow-striped | | gy | |
| Non-anthocyanin colors of glumes in presence of Gh | Hf | df | $H^m$, $H^i$, $H^g$, $H^f$ |
| Helminthosporium resistance | Le, Om | Hm, Le | He |
| hullspot | | | hsp |
| Positive staining with KI-I solution | | | I |
| Inhibitor gene | | | I- |

| Character expression | Kadam & Ramiah (1943) | Nagao (1951) | IRC (1959), Anon. (1963), Chang & Jodon (1963) |
|---|---|---|---|
| lethal character | | | l- |
| lazy or ageotropic | la | la | la |
| Lodging of culms | Ld | Ld | Ld |
| Late flowering (highly photosensitive) | Fl | | Lf |
| liguleless | lg | lg | lg |
| Heavy pubescence | Lh | | Lh |
| long grain | kl | g | lk |
| Long panicle | | Lp | |
| lutescent | l | lu | lu |
| Lax (vs. normal panicle) | Lx | | Lx |
| Lax (vs. compact panicle) | | | Lx2 |
| multiple embryos (polyembryonic) | | | me |
| Minute spikelet | | Mi | |
| multiple pistils (polycaryoptic) | mp | mp | mp |
| male sterile | fm | ms | |
| narrow leaf | | | nal |
| neck leaf | | | nl |
| notched kernel | | | nk, or I-Nk |
| open hull (parted lemma and palea) | hpt | op | o |
| Ophiobolus miyabeanus (or Helminthosporium oryzae) resistance | Om | | |
| Purple apiculus | Ap | Sp (later A) | P (with C & A) |
| paleaceous sterile | fp | pas | |
| Purple auricle | Aup | | Pau |
| Purple outerglumes | Gp | | Pg |
| Phenol staining | | Ph | Ph |

| Character expression | Kadam & Ramiah (1943) | Nagao (1951) | IRC (1959), Anon. (1963), Chang & Jodon (1963) |
|---|---|---|---|
| Piricularia resistance | Pi | Pi | Pi |
| Purple internode | Ntp | Pnt | Pin |
| Purple junctura | Jp | | Pj |
| Purple leaf | Lp | Pl | Pl |
| Purple leaf apex | | | Pla |
| Purple ligule | Lgp | | Plg |
| Colorless leaf except margin | Lmp | Pla | I-Pl |
| Purple midrib (or leaf axil) | Lxp | Plm | |
| Purple node | Np | Pn | Pn |
| Purple hull | H-p | Rp | Pr |
| Purple root | Rp | Pr | |
| Purple pericarp | Prp | Pp | Prp |
| Purple stigma | Sp | Ps | Ps (with C, A & P) |
| Purple leaf sheath | Lsp | Pls | Psh |
| Purple pulvinus | | | Pu |
| Purplewash | | | Pw |
| Purple axil | Lxp | | Px |
| Red awn | Anr | | Ran |
| Brown pericarp | Pbr | Rc | Rc |
| Red pericarp | Pr | Rd | Rd (with Rc) |
| verticillate (whorled) arrangement of rachis | | | ri |
| Round spikelet | Kr | Rk | Rk |
| rolled leaf | lro | rl | rl |
| sterility (general) | f | s | s |
| Sclerotium oryzae resistance | | | Sc |
| Seed dormancy | | | Sd |
| Photosensitivity | | | Se |

| Character expression | Kadam & Ramiah (1943) | Nagao (1951) | IRC (1959), Anon. (1963), Chang & Jodon (1963) |
|---|---|---|---|
| Permeability of testa to water | | | Sg |
| Shattering | Sh | Sh | Sh |
| Scented kernel | O | Sc | Sk |
| sinuous neck | ne | ne | sn |
| spreading panicle | spr | Sg | spr |
| semi-sterile | fs | ss | |
| staminoidal sterile | fst | sts | |
| Tallness (height in general) | T | | T |
| short non-dwarf plant (vs. tall) | It | | I-T |
| Difficult dehulling | Tf | to | Tf |
| easy threshing | | | th |
| long twisted kernel | | | tk |
| twisted leaves (no midrib) | ltw | tw | tl |
| triangular hull (spikelet) | | th | tri |
| Undulate rachis | | | Ur |
| virescent seedling or green-and-white stripe | v | v or gs | v |
| variegated seedling | vr | vr | |
| vitreous (vs. opaque grain) | Op | | |
| white belly (endosperm) | wb | ab | wb |
| white core (endosperm) | | | wb2 |
| White hull | h-w | | Wh |
| white stripe | | | ws |
| waxy (glutinous) endosperm | wx | gl | wx |
| Xanthomonas oryzae resistance | | | Xe |
| yellow leaf | | | y |
| lethal yellow (xantha) | y | xa | l-y |
| zebra stripe | z | | z |

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